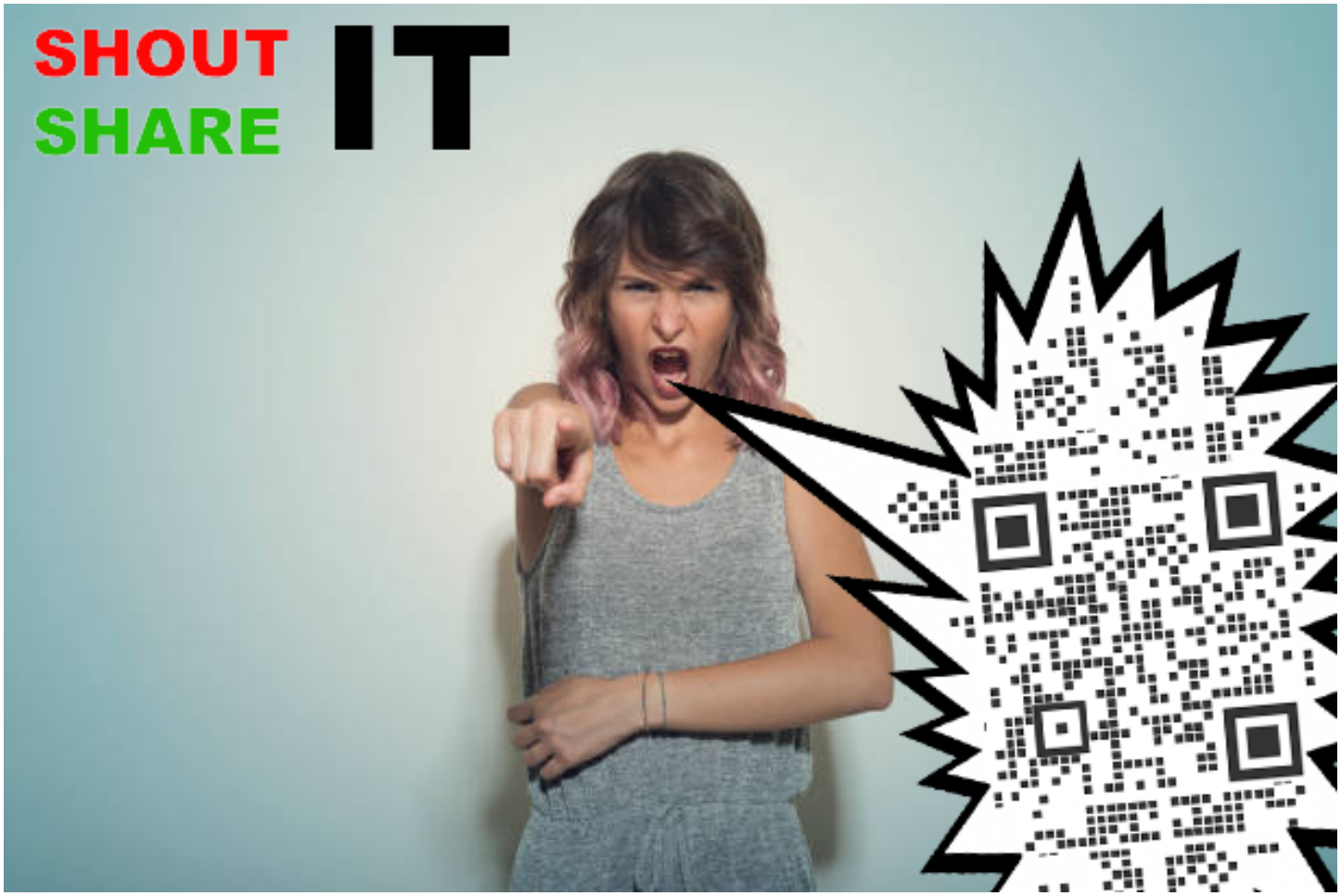
SBM·1010

BRITISH MUSEUM
(NATURAL HISTORY)
11 DEC 1991
PRESENTED
GENERAL LIBRARY

Bulletin British Museum (Natural History)

Botany Series

VOLUME 21 NUMBER 2 28 NOVEMBER 1991


SHOUT
SHARE
IT

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

The Botany Series is edited in the Museum's Department of Botany

Keeper of Botany:	Dr S. Blackmore
Editor of Bulletin:	Dr R. Huxley
Assistant Editor:	Mrs M. J. West

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

A volume contains about 256 pages, made up of two numbers: published Spring and Autumn. Subscriptions may be placed for one or more of the series on an annual basis. Individual numbers and back numbers can be purchased and a Bulletin catalogue, by series, is available. Orders and enquiries should be sent to:

Sales Department,
Natural History Museum Publications,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD

Telephone: 071-938-9386
Fax: 071-938-9212

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Bot.)

© British Museum (Natural History), 1991

ISBN 0 565 08029 6
ISSN 0068 – 2292

Botany Series
Vol **21**(2), pp 81 – 194

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 28 November 1991

Typeset by Waveney Typesetters, Norwich, Norfolk.
Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

Bull. Br. Mus. nat. Hist. (Bot.) **21**(2) 81–83 Issued 28 November 1991

Early collections of the Holy Thorn (*Crataegus monogyna* cv. Biflora)

BRITISH MUSEUM
(NATURAL HISTORY)
11DEC1991
PRESENTED
GENERAL LIBRARY

A. R. Vickery

Department of Botany, The Natural History Museum, Cromwell Road, London, SW7 5BD.

Commonly known as the Holy Thorn, or Glastonbury Thorn, *Crataegus monogyna* Jacq. cultivarietas Biflora (syn. *C. oxyacantha* var. *praecox* Loudon) differs from typical *C. monogyna* in that it produces flowers in winter as well as at the usual time, in early summer, each year. A full account of the history and legends associated with the plant is given in Vickery (1979).

Crataegus monogyna cv. Biflora has been known since 1535 (Batten, 1881), or possibly earlier, for a poem (Anon., 1520) written in the early years of the sixteenth century appears to refer to it. This poem mentions three *Crataegus*—'thorn'—trees growing on Wearyall Hill, south-west of Glastonbury in Somerset, south-west England, which bear leaves at Christmas (25 December), but makes no mention of winter flowers. The most common of the legends associated with the plant tells how the Apostles divided the world between them, with St Philip accompanied by St Joseph of Arimathaea being sent to Gaul. After some years St Joseph set out for Britain, arriving at Glastonbury and founding the first church to be built on British soil in AD 63 (Hole, 1965). When St Joseph reached Glastonbury he rested on Wearyall Hill thrusting his dry staff into the ground, whereupon it budded, produced blossoms, and became the original Holy Thorn (Rawlinson, 1722).

According to some versions of the legend, the flowering of St Joseph's staff took place on Christmas Day, and descendents of the tree which grew from the staff have flowered on that day ever since. Thus after the Gregorian calendar was adopted in 1752, when 11 days were 'lost' in September, people gathered around the various Thorn trees growing in Glastonbury to see if they would produce flowers according to the new calendar (24 December) or the old (5 January). It seems that then, as now, the trees produced a steady number of flowers throughout the winter, for there are conflicting reports of the 1752/53 observations (Anon. 1753).

The earliest specimens of the Thorn in the herbarium of the Natural History Museum are in the herbarium of Leonard Plukenet (1642–1706), now included in the Sloane Herbarium (H.S. 83, f.269). One of these specimens consists of four detached leaves labelled '*Oxyacant, Avilonsis* . . .' The other specimen, mounted on the same sheet, consists of the tip of a twig bearing three complete, and one apparently incomplete, leaves, labelled 'Glassenburrow Thorn'. The leaves of this specimen are certainly atypical for *Crataegus monogyna* and bear a closer resemblance to those of *C. laevigata* (Poiret) DC. or to some New World species of *Crataegus*, so the identity of this specimen must remain uncertain. However, it is known that during the seventeenth century the Glastonbury tree, or trees, were severely mistreated, being hacked down by puritans (Taylor, 1649) and mutilated by tourists seeking souvenirs (Eachard, 1645), so it is not improbable that such long suffering trees might have produced abnormal foliage.

The sheet illustrated in Fig. 1 has three eighteenth century specimens of *Crataegus monogyna* cv. Biflora mounted on it. Two of these, mounted on the top left-hand corner of the sheet, formed part of the herbarium of Sir Joseph Banks (1743–1820). The ink label accompanying these, in the hand of Jonas Dryander who was employed by Banks from 1778–1820, has been cut from the back left-hand corner of the original sheet. The pencilled label placed below this is in the hand of Daniel Carl Solander who was employed as Banks' Curator-Librarian from 1771–1782, and was formerly at the lower front margin of the original sheet.

The smaller of the two specimens—1. Anglia: Glastenbury. St. Alchorne—was collected by Stanesbury Alchorne (1727–1800), an apothecary and officer at the Mint, who served as honorary Demonstrator of Plants at the Chelsea Physic Garden from the spring of 1771 until December 1772 (Field, 1820). It seems that Alchorne had a special interest in *Crataegus* for during his short time as Demonstrator he presented to the Garden 'nearly fifty new trees, particularly of the Crataegi, Mespili and Pini Genera' (Field, 1820).

The larger specimen, bearing both leaves and flowers—2. Hort.—is from an unidentified garden. However, Britten (1913) states that specimens in the Banks' herbarium labelled 'Hort.' can be assumed to be from the herbarium of Philip Miller (1691–1771) if there is a pencil tick against their name in Banks' copy of the eighth (1768) edition of Miller's *Gardeners Dictionary*. This volume, now in the Botany Library of the Natural History Museum, has been examined. The only entry which mentions the Holy Thorn reads: 'GLASTENBURY THORN. see MESPILUS', but nothing relevant can be found under *Mespilus*. In the seventh (1759) edition of the *Dictionary* Miller lists the common hawthorn (i.e. *C. monogyna*) as his third species of *Mespilus*, and provides two sentences about the Holy Thorn, concluding 'but stories which are told of its budding, blossoming and fading on Christmas Day, are ridiculous having no foundation'. In the eighth edition the common hawthorn becomes the eighth species to be listed under *Crataegus,* but no mention is made of the Holy Thorn. Thus it appears that the cross reference 'GLASTENBURY THORN. see MESPILUS' should have been deleted from this edition. As the eighth species of *Crataegus* has a pencil tick, and no other specimen of *C. monogyna* which can be associated with Miller can be found, it is possible that this specimen was originally in the Miller herbarium, and possibly collected from a tree which grew in the Chelsea Physic Garden during Miller's curatorship of the Garden between 1722 and 1770.

The third specimen on the sheet is from the herbarium of the London apothecary Robert Nicholls (fl. 1713–1750), which was given by him to the Apothecaries' Company in 1745, and formed part of a 'valuable series of plants' presented by the Company to the Museum in 1862 (Anon. 1904). The ink label is apparently in Nicholls' hand, and although it states 'from Wells', the specimen was most probably collected from Glastonbury, some 8 km south-west of Wells.

Fig. 1 Herbarium sheet with three eighteenth century collections of *Crataegus monogyna* cv. Biflora (BM).

Other writing on the sheet cannot be identified with any certainty, although the 'Herb. R. Nicholls, 1745' appears to be in the hand of James Britten (1846–1924), who worked in the Museum's Department of Botany, taking a great deal of interest in its historic collections, from 1871 until his death. The 'V.C. 6' was written on the sheet when it was housed in the Museum's British Herbarium, and refers to the vice-county 6 (North Somerset) of the system devised by H. C. Watson in 1852 for recording the geographical distribution of British plants (see Dandy, 1969).

Finally, the specimens have been critically determined by Carl Axel Magnus Lindman (1856–1928) in 1912, and by K. I. Christensen in 1988. Being primarily concerned with taxonomy of wild plants, neither Lindman nor Christensen have taken interest in the cultivar Biflora, and have been satisfied to identify the specimens as typical *C. monogyna*. As all three specimens appear to have been collected during the summer it is impossible to know if, in fact, they belong to the cultivar, unless one relies on the information supplied on the sheet.

Today a young Thorn tree, windswept and protected by metal railings, can be found on Wearyall Hill and various other trees which are supposedly descended from the original tree are found around the town. Particularly noteworthy are the trees growing in the Abbey grounds, and the tree in St John's churchyard (Vickery, 1979).

ACKNOWLEDGEMENTS. Thanks are due to J. B. Marshall for the identification of handwriting, to Ruth Stungo for information on Alchorne, and to J. R. Laundon for his comments on an early draft of the manuscript.

Note added in proof: The tree in St John's churchyard died in early 1991.

REFERENCES

Anon. 1520. *Here begynneth the life of Joseph of Armathia*. London.
Anon. 1753. *The Gentleman's Magazine* 23: 49, 578.
Anon. 1904. *The history of the collections contained in the Natural History Departments of the British Museum*. **1**. London.
Batten, E. C. 1881. The Holy Thorn of Glastonbury. *Proc. Somerset Archaeol. Nat. Hist. Soc.* 26 (2): 118–125.
Britten, J. 1913. Philip Miller's plants. *J. Bot.* **51:** 132–135.
Dandy, J. E. 1969. *Watsonian Vice-Counties of Great Britain*. London.
Eachard, J. 1645. *Good news for all Christian soldiers*. London.
Field, H. 1820. *Memoirs, historical and illustrative of the Botanick Garden at Chelsea*. London.
Hole, C. 1965. *Saints in folklore*. London.
Miller, P. 1759. *The gardeners dictionary*, Ed. 7. London.
—— 1768. *The gardeners dictionary*. Ed. 8. London.
Rawlinson, R. 1722. *The history and antiquities of Glastonbury*. Oxford.
Taylor, J. 1649. *John Taylor's wandering to see the wonders of the West*. London.
Vickery, A. R. 1979. *Holy Thorn of Glastonbury*. St Peter Port.

Bull. Br. Mus. nat. Hist. (Bot.) **21**(2): 85–192 Issued 28 November 1991

A taxonomic study of the species referred to the ascomycete genus *Leptorhaphis*

BEGOÑA AGUIRRE-HUDSON

58 Willowhayne Drive, Walton on Thames, Surrey KT12 2NR

CONTENTS

Introduction 86
History of the usage of the generic name 86
Material 88
Methods 88
Taxonomic concepts 88
Vegetative thallus 88
Ascomata 89
Hamathecium 89
Asci 90
Ascospores 91
Conidiomata 91
Biological concepts 92
Taxonomic relationships 92
Key to the genera 93
I. *Leptorhaphis* Körber 94
Key to the species 97
The species 97
II. *Arthopyrenia* Massal 123
The species 124
III. *Celothelium* Massal 131
Key to the species 132
The species 134
IV. *Cresporhaphis* Aguirre 146
Key to the species 147
The species 147
V. *Rhaphidicyrtis* Vainio 156
The species 156
VI. *Sarcopyrenia* Nyl 158
Key to the species 159
The species 159
VII. Excluded or uncertain taxa 164
References 187
Index 189

SYNOPSIS. Several hundred specimens including types of the taxa traditionally referred to the genus *Leptorhaphis* Körber were studied morphologically during the course of this research, and nomenclatural, ecological, and distributional considerations were discussed for each taxon. The generic concept as currently accepted proved to be heterogeneous, and many of the 63 specific epithets included were found to be referable elsewhere. Only 12 species have been accepted as congeneric, characterized by dimidiate pseudoparaphysate ascomata and fusiform-arcuate ascospores. These species are bark saprobes, only occasionally associated with trentepohlioid algae, and are characteristic components of pioneer lichen communities on bark. The genus thus delimited clearly belongs to the family Arthopyreniaceae in the order Dothideales. No new species are described, but the following new combination is proposed: *Leptorhaphis laricis* (Lahm) Aguirre comb. nov.

The remaining taxa have been referred to genera belonging to different families or even orders, and in some cases their systematic positions still remain uncertain until ontogenetic studies are carried out. For some of the taxa it has been necessary to re-establish two genera : *Celothelium* Massal. and *Raphidicyrtis* Vainio, both with an uncertain position amongst the Pyrenulales, and including species with very long, filiform ascospores, paraphysoids in the hamathecium, and mainly lichen-forming with trentepohlioid photobionts. The following new combinations are made: *Celothelium buxi* (Steiner), *C. dominicanum* (Vainio), *C. ischnobelum*× (Nyl.), and *C. stenobelum* (Nyl.) Aguirre combs nov.

A new generic name, *Cresporhaphis* Aguirre is proposed for several species with entire ascomata, very thin wall-layered asci ('unitunicate'), and lichen-forming, associated with an unidentified photobiont. The following new

combinations are suggested: *Cresporhaphis acerina* (Rehm), *C. macrospora* (Eitner), *C. muelleri* (Duby), *C. pinicola* (G. Samp.), and *C. wienkampii* (Lahm ex Hazslin) Aguirre combs nov.

The generic concept of *Sarcopyrenia*, traditionally regarded as a monotypic genus, is here extended to two more taxa, *S. beckhausiana* (Lahm) Aguirre, Nav.-Ros. & Hladún and *S. cylindrospora* (P. Crouan & H. Crouan) Aguirre. Finally, new combinations are proposed for three excluded species : *Rhytidiella beloniza* (Stirton), *Stictis candida* (Steiner), and *Capronia longonigra* (Norman) Aguirre combs nov.

INTRODUCTION

Criteria such as ascomatal colour or ascospore colour and septation, introduced by de Notaris (1846), became predominant during the nineteenth century and early decades of this century in the taxonomy and classification of the fungi. Such criteria often ignored other features of ascoma structure, and as a result unrelated taxa were often placed together in the same genus or family, whereas other taxonomically related taxa were dispersed amongst uncorrelated groups. *Karschia* (Hafellner, 1979), *Microglaena* (Mayrhofer & Poelt, 1985), and *Microthelia* (Hawksworth, 1985*a*) are examples of genera which included unrelated taxa, and *Micarea* (Coppins, 1983) one in which members were scattered over several genera on the basis of spore septation. Similar cases are discussed by Sherwood (1981) for genera of lignicolous discomycetes. Spore septation and colour have proved to be unsatisfactory for the a priori recognition of monophyletic genera since these characters can be modified by convergent evolution, and are not therefore necessarily indicative of systematic relationships between groups, nor of their biology (Hawksworth, 1985*b*).

The main objective of this contribution, by using more critical taxonomic criteria, is to assess whether the taxa referred to *Leptorhaphis* Körber, a genus neglected in recent decades, form a natural grouping or not, and to provide a modern treatment. Almost from the beginning it became apparent that the group was heterogeneous, and a preliminary contribution on the generic delimitations, biology and taxonomic relationships was presented by Aguirre & Hawksworth (1987). Of 63 epithets currently in *Leptorhaphis*, only 12 species are accepted as congeneric here. The remainder have been distributed among other existing genera, such as *Arthopyrenia*, *Celothelium*, *Sarcopyrenia* or *Rhaphidicyrtis*; it was also necessary to introduce a new generic name, *Cresporhaphis*, to accommodate some of the taxa.

This study has been based primarily on morphological characters. Although laboratory cultures of fresh material of *Leptorhaphis epidermidis* were attempted, these always proved unsuccessfull. Aspects such as ontogeny or ultrastructure were not pursued in depth during the course of this research, but in the future can be directed towards the genera now recognized. These, and aspects such as cytology, genome compatibility, or coevolutionary considerations are now regarded as of particular importance in the systematics of lichenized or not lichenized groups (Hawksworth, 1985*b*; 1988*b*). Ontogenic studies especially are needed to clarify the uncertain systematic position of several groups discussed here.

The generic delimitations here presented should be primarily regarded as clarification of the taxonomy of the names referred to *Leptorhaphis* at the generic level to bring them into accord with modern revisions of other groups of ascomycetes.

HISTORY OF USAGE OF THE GENERIC NAME

The generic name *Leptorhaphis* (Gk λεπγός, slender, delicate; ρ∝φίς, needle) was first introduced by Körber (1855: 371) within the family Verrucariaceae in his work *Systema lichenum Germaniae*, for *Arthopyrenia*- like species with acicular ascospores. Thus, he followed the criteria of de Notaris (1846) and other contemporary authors in recognizing the importance of ascospore morphology and colour for the classification of both lichenized and non-lichenized fungi at generic level. He recognized two species in the genus: *Leptorhaphis oxyspora* (Nyl.) Körber [i.e. *Leptorhaphis epidermidis* (Ach.) Th. Fr.] on *Betula* bark, and *Leptorhaphis tremulae* Körber on *Populus* bark. His choice of Nylander's specific epithet *'oxyspora'* in preference to the earlier *Verrucaria epidermidis* Ach. was occasioned by already existing confusion over the application of the epithet *'epidermidis'*, which had been misused for various *Arthopyrenia*-like species on birch bark. Nevertheless, these arguments were not accepted by Th. Fries (1860: 373), who a year later (1861: 111) selected the earlier name *Lichen epidermidis* Ach. as an 'example' of the genus *Leptorhaphis*. Later this has been regarded, and is accepted here, as the first lectotypification of the generic name.

Almost at the same time, the Italian mycologist Massalongo (1856: 184) erected the genus *Campylacia*, based on identical criteria of ascospore morphology used by Körber. He had introduced the name on the previous year as a subgenus [*Sagedia* subg. *Campylacia* Massal., 1855: 96] with a short diagnosis in Italian. Altogether he described five taxa, one of which had been already treated by Körber, and accepted by Massalongo as *Campylacia tremulae* (Körber) Massal. [syn. *Sagedia salicis* Massal.], which is conspecific with *Leptorhaphis atomaria* (Ach.) Szat. He also suspected that these taxa were not lichenized, recognizing them as saprobes, which on occasion can be associated with green 'gonidia' (i.e. algae). All his new taxa are still accepted within the modern concept of the genus *Leptorhaphis*.

A third generic name *Endophis* had been introduced a few years earlier by Norman (1853: 240) for a single species, but this was overlooked by most contemporary and later lichenologists, and although the characteristics of the genus were clearly defined. *Leptorhaphis* Körber was accepted for conservation over *Endophis* (Lanjouw et al., 1956: 212), following the recommendation of Zahlbruckner (1935: 128), on the basis that Norman did not designate a satisfactory type, citing *Endophis cerasi* 'auct. pr.p.'. Norman's failure to select a type for *Endophis* was also noted by Th. Fries (1861: 111), and later Norman himself (1868: 192; 1884 : 40) also accepted the application of the generic name *Leptorhaphis* describing some additional species within the genus; interestingly on the packet of one of these, *L. xylographoides*

Norman [i.e. *Leptorhaphis parameca* (Massal.) Körber], the name '*Endophis cerasi*' was also written (see p. 00, 00).

Some Italian authors, such as Beltramini (1858), continued to use Massalongo's genus *Campylacia* rather than *Leptorhaphis*, but others such as Trevisan (1860) in his treatment of the verrucariaceous fungi, grouped within *Sagedia* Fée several accepted genera, *Leptorhaphis* Körber and *Campylacia* Massal. amongst others. The corticolous species with acicular to fusiform and multilocular ascospores were treated by him as a distinct section of *Sagedia*. Authors with broader generic concepts, such as Nylander (1858) and Müller Argoviensis (1862), did not recognize either *Leptorhaphis* or *Campylacia*, and included the species in *Verrucaria* or *Arthopyrenia* respectively, sometimes as a section, e.g. *Arthopyrenia* sect. *Leptorhaphis* (Körber) Müll. Arg.

Körber (1865: 384) established the priority of *Leptorhaphis* over *Campylacia*, which he considered to have been introduced without a proper diagnosis, broadening the concept of the genus by including three more species: *Leptorhaphis lucida* Körber, *L. wienkampii* Lahm [i.e. *Cresporhaphis wienkampii* (Lahm) Aguirre], and the saxicolous *L. beckhausiana* Lahm [i.e. *Sarcopyrenia beckhausiana* (Lahm) Aguirre, Nav.-Ros. & Hladún]. The latter species was probably accepted by Körber in *Leptorhaphis* despite recognized external similarities with the genus *Lithosphaeria* Lahm (*in* Körber, 1863: 344; a superfluous name for *Sarcopyrenia* Nylander, 1858), because of its filiform ascospores, lacking the characteristic capitated apices of *Lithosphaeria geisleri* Beckh. [i.e. *Sarcopyrenia gibba* Nyl.].

The following decades saw an increase in the number of species being ascribed to the genus on the basis of filiform ascospores. This was the case with some of the tropical species referred to the genus by Vainio (1890: 230), such as *Leptorhaphis aciculiferum* (Nyl.) Vainio [i.e. *Celothelium aciculiferum* (Nyl.) Vainio] and *L. cinchonarum* (Müll. Arg.) Vainio [i.e. *Celothelium cinchonarum* (Müll. Arg.) Vainio], first described from Brazil as *Melanotheca* and *Tomasellia* species respectively. There, Vainio (op. cit.) recognized two subgenera in *Leptorhaphis*: subgen. *Campylacia* for species with uniloculate ascomata, and subgen. *Tomasellia* for ones with multiloculate ascomata.

Nevertheless, Vainio (1915) later approached this group differently, delimiting *Leptorhaphis* as a non-lichenized fungal genus, referring the two previously included species to the genus *Celothelium* Massal. This latter name had been introduced by Massalongo (1860: 332) for a tropical species with filiform ascospores and confluent ascomata. Vainio (1915: 210) also described a new taxon in *Leptorhaphis*, *L. dominicana* [i.e. *Celothelium dominicanum* (Vainio) Aguirre], which seemed not to be associated with any algae.

Following this view, Vainio (1921), in his study of the Finnish lichenized pyrenocarps, regarded the genus as non-lichenized, but then he accepted the species under Massalongo's generic name *Campylacia*, pointing out possible affinities with the non-lichenized genus *Ophiobolus* Riess, characterized by filiform multiseptate ascospores (Walker, 1980). Vainio's most pertinent contributions to the clarification of the genus in this work were the detailed study and notes on the holotype of *Lichen epidermidis* in the Acharian herbarium at Helsinki, and the lectotypification of *Lichen atomarius* Ach. for some taxa included within the concept of *Leptorhaphis tremulae* Körber. Indeed, Vainio regarded the latter as a superfluous name for *Lichen atomarius* [i.e. *Leptorhaphis atomaria* (Ach.) Szat.], but my comparative studies of both taxa sets them apart; *Leptorhaphis tremulae* Körber is the correct name for another species, *Campylacia sphenospora* (Nyl.) Vainio, mentioned by Vainio in his generic account.

A decade earlier Clements (1909) had issued the first edition of his seminal work, *The Genera of Fungi*. In this *Leptorhaphis*, in common with *Arthopyrenia*, was recognized as a genus with more than 1-septate ascospores limiting those taxa with 1-septate ascospores to a newly erected genus *Pyrenyllium* Clem., typified by *Lichen analeptus* Ach., a name of uncertain application (see p. 96, 124).

North American studies of the genus in the beginning of this century included that of Fink (1910), who cited *Leptorhaphis epidermidis* (as '*Sagedia oxyspora* (Nyl.) Tuck.') within the family Pyrenulaceae, together with genera such as *Arthopyrenia*, *Verrucaria*, and *Pyrenula*, all of which he considered as closely related.

Zahlbruckner (1921–22, 1932) in his *Catalogus lichenum universalis*, accepted altogether 36 taxa in *Leptorhaphis*, 32 at the rank of species, mostly described from the Northern Hemisphere, with only a few tropical species such as *Leptorhaphis dominicana* Vainio [i.e. *Celothelium dominicanum* (Vainio) Aguirre]. However, he did not recognize the genus *Celothelium* and placed the taxa included in it by Vainio (1915) within *Tomasellia*. Also, he maintained the epithet '*atomaria*' for an *Arthopyrenia* species, disregarding or overlooking Vainio's lectotypification.

The most significant previous contribution to our knowledge of *Leptorhaphis* was, however, Keissler's (1938) critical study of the central European species; he appreciated marked variations in ascomatal structure, iodine reaction of the centrum hymenial gelatin, and ascospores, although he maintained a broad generic concept. He divided the genus in two sections, *Leptorhaphis* sect. *Integrae* and *Leptorhaphis* sect. *Dimidiatae*, based on entire or dimidiate ascomata, which are regarded as of generic rank here. These sections approximately correspond to the species included in the genus *Cresporhaphis* Aguirre described here, and in *Leptorhaphis s. str.* respectively. Concern about the fact that he could not see a clearly developed lichen thallus in some species led Keissler to investigate the possible relationships of these taxa with species of *Ophiobolus* Riess or *Leptosphaeria* Ces. & de Not. Thus, he redisposed satisfactorily *Leptorhaphis steinii* Körber, which he believed to be taxonomically identical to *Ophiobolus barbarus* (Th.Fr.) Keissler [i.e. *Sagediopsis barbara* (Th.Fr.) R. Sant. & Triebel], and was first to suggest the affinities within *Sarcopyrenia* of *Leptorhaphis beckhausiana* [i.e. *S. beckhausiana* (Lahm) Aguirre, Nav.-Ros. & Hladún], although he failed to validate the combination. Modern European lichen floras, such as those of Wirth (1980) and Clauzade & Roux (1985), have followed Keissler's criteria for the grouping of the species and their differentiation.

More recent critical studies were carried out by Swinscow (1965) in the British Isles, and by Harris (1973) in North America, both of whom stressed that the genus should not be regarded as lichen-forming. Especially important is the latter's contribution to the taxonomic and systematic clarification of the genus in North America, with detailed descriptions of the four species recognized in the area, and their typification. These studies helped to delimit a new taxonomic concept of the genus, later developed by Aguirre & Hawksworth (1987), and adopted here.

MATERIAL

Type material, and additional collections where available, have been studied during the course of this research. Type material was kindly provided on loan by the following institutional herbaria: B, BM, BP, C, Concarneau, CUP, E, G, H, K, L, LD, LISU, M, O, PAD, PC, S, TCN, TUR, UPS, VER, W, WELT, WRSL, and Degelius personal herbarium (abbreviations follow Holmgren et al., 1981), and in some cases studied *in situ*.

Additional material from B, BM, E, IMI, O, and PC was also studied, IMI in particular being a very valuable source of information for both related and unrelated taxa, and serving as a comparative basis for the redisposition of many of those which were excluded from *Leptorhaphis*.

In total about 700 specimens were critically studied during the course of this investigation. Only *Leptorhaphis epidermidis* was examined in fresh condition, having been collected in the British Isles, France, and Sweden. These fresh specimens provided additional information on the ecology of the taxon, as well as material for culture experiments.

METHODS

Preliminary studies of the literature cataloguing lichen names, such as Zahlbruckner (1921–22, 1932), Lamb (1963) and the *Index of Fungi* (1970–), provided the initial information on the places of publication for names referred to *Leptorhaphis*.

For routine microscopic examination, individual ascomata were dissected from the specimen in blocks of the substratum and embedded in a dilute solution of gum arabic to soften them for a few (never over 12) hours. They were then sectioned in the same solution with a Reichert Mectron freezing microtome set at 10 μm. Sections were transferred to water, and mounted directly in lactophenol cotton blue or lactofuchsin (Johnston & Booth, 1983: 400), being sealed with Glyceel, a cellulose-based sealant for permanent or semi-permanent slides, after being warmed (Hawksworth, 1974: 21).

Squash mounts and hand sections were also prepared to facilitate the examination of individual asci and ascospores. The mounting medium used in this case was 10% KOH, which tends to soften old herbarium material and is a necessary pre-treatment for obtaining satisfactory and repeatable reactions of hamathecial and ascal tissues preceding Lugol's iodine (Nannfeldt, 1976: 283–287; Hawksworth et al., 1983; Baral, 1987: 399–450). The technique also permits a better study of the apical apparatus in asci. Occasionally Melzer's iodine solution (Hawksworth et al., 1983) was used when the hymenial gelatin reaction was negative, but this was later abandoned since it did not yield additional information. Later lactophenol cotton blue was run into the slide to assure its semi-permanent preservation, heated, and sealed (Dring, 1971: 99). Conidiomata, conidiogenous cells and conidia were also studied through squash mounts in lactofuchsin and similarly heated for a few seconds as with cotton blue to reduce significant differences that can arise from the use of different mountants (Oliver et al., 1987: 171).

Measurements were made with a micrometer eyepiece fitted in the microscope at ×1250 and based on free ascospores mounted in heated lactophenol cotton-blue, except in the genus *Celothelium*, where sometimes they had to be taken inside the asci since it was difficult to observe intact free ascospores. Where possible ten ascospores minimum were measured and drawn for each specimen.

On occasion the material was mounted in a solution of 0.5g erythrosin in 100 ml of 10% ammonia and Congo red, which has been shown to improve detailed study of ascus structure in other groups (Minter & Cannon, 1984: 67; Eriksson, 1981: 13); indian ink was used to detect hyaline ascospore appendages (Lundqvist, 1972: 13); and nitric acid in low concentration (about 15%) was used to test for changes in colour of the involucrellum (Harris, 1973: 5), such as those known in *Mycoglaena myricae*.

Drawings of asci, and ascospore outlines, were prepared with a Leitz Wetzlar microscope fitted with a drawing tube, and microphotographs taken on Kodak PAN X film, using a Zeiss Photomicroscope Universal equipped with Nomarski differential interference contrast optics. A few specimens were also examined with a Hitachi S-570 SEM, and microphotographs taken on Kodak Plus PAN X film, of individual and sectioned air-dried ascomata, mounted on aluminium stubs and coated with gold, for the purpose of elucidating wall structures and textures.

Cultures of fresh material of *Leptorhaphis epidermidis* were also prepared, and two different spore isolation techniques were used: the 'discharge chamber' (Ahmadjian, 1974), and a somewhat modified 'dilution plate' method (Booth, 1971). Ascospore germination was tested in various agar media although not bark extract, and mainly in TWA and MYE. Due to the lack of germination at room temperature, artificial stimuli such as heat- and cold-shock, or chemicals were asseyed to break ascospore dormancy (Sussman & Halvorsson, 1966; Booth, 1971). However, these experiments also failed, although ascospore swelling was observed after two weeks, probably due to water absortion from the medium. After five or six weeks the plates were finally discarded.

TAXONOMIC CONCEPTS

Vegetative thallus

In the majority of the Arthopyreniaceae, and particularly in the genus *Leptorhaphis* a differentiated vegetative thallus is absent or represented only by paler lighter areas on the surface of the bark, arising by trapped air, and provides little or no information of taxonomic value (Harris, 1975). In vertical section fungal filaments can be distinguished only with difficulty among the bark cells, with which they are closely associated.

However, in some genera such as *Celothelium* and *Rhaphidicyrtis*, both provisionally referred to the Pyrenulales, fungal hyphae are intimately associated with trentepohlioid filaments below the bark surface forming a smooth to somewhat pulveraceous crustose thallus. Colour and texture of the thallus were found to differ between the species of the genus. On occasions, the presence or absence of a delimiting prothallus was used as a taxonomic characteristic to delimit the

species in *Celothelium*. The term prothallus is used here following Hawksworth et al. (1983) as 'the first hyphae of the thallus to grow, usually used of a crustaceous lichen which had no algal cells or cortex'.

Ascomata

While ontogenetic studies have not been carried out for *Leptorhaphis* or any of its segregates, Janex-Favre (1968) studied the ontogeny of *Arthopyrenia*, in *A. lapponina* Anzi [syn. *A. fallax* (Nyl.) Arnold], and found that this could be regarded as a typical pyrenomycete with ascolocular development, where the carpocentre is produced by a pseudoparenchymatous structure called stroma and the sporophyte is surrounded by a system of pseudoparaphyses. In vertical section mature ascomata of *Leptorhaphis* in vertical section show many similarities to the fully developed ascomata of *Arthopyrenia lapponina* as represented by Janex-Favre. The ascomata initially develop beneath the surface of the substratum, becoming erumpent through cracks or superficial, where the stromatic covering wall might or finally might not incorporate host tissue (clypeus). This covering wall, here termed the involucrellum, is always present in *Leptorhaphis*, and in some species, for example *L. epidermidis* and *L. parameca*, can extend beyond the ascomata forming a basal fringe. The presence or absence of a basal fringe, and sometimes its width, has been used as an additional character to differentiate the species in *Mycomicrothelia* (Hawksworth, 1985*b*). However, this character has to be used with caution since the ability of the fungus to produce a basal fringe might in part result from a response mechanism to the nature of the substratum. In addition to the involucrellum, some species develop a more or less differentiated exciple, which surrounds the generative locule, and can occasionally extend below.

The position of the ascomata was regarded by Eriksson (1981) as of taxonomic importance at the specific or generic level, and sometimes at higher levels. However, Harris (1975) deliberately avoided these characters since he believed that they can be subject to environmental modification. Nevertheless, the character proved of value at both the specific and generic level in the present study, combined with other characters, such as ascus and ascospore morphology and size. Some species in the genus *Cresporhaphis*, such as *C. wienkampii* and *C. muelleri*, are always superficial, emerging or not from cracks, whereas *C. acerina* always remains half-immersed in the substratum. On the other hand, ascomata of *Leptorhaphis* remain immersed in the substratum to a greater or lesser extent, whereas in the genus *Rhytidiella* (e.g. *R. beloniza*) these are always superficial.

Ascomata may be also multilocular, and sometimes this can result from the enclosure of several uniloculate ascomata by a common pseudostroma or involucrellum. The structure thus developed was called a 'synascoma' by Eriksson (1981). He further defined pseudostromata as 'thalline tissue plus the remnants of host tissue', which were observed more or less developed in *Celothelium*, and have been described for other members of the Pyrenulales, such as the Trypetheliaceae and many other 'bitunicates' (Eriksson, 1981).

Although the ascomata in *Leptorhaphis* are perithecium-like (perithecioid) and have a stromatic origin, a few species previously referred to the genus have apothecioid ascomata, e.g. *Stictis* and *Odontura*. The morphology and development of these apothecioid ascomata of these genera has been described and discussed in detail by Sherwood (1977*a*,*b*), and her terminology was used for the description of these taxa; their fruit-bodies are 'deeply urceolate and immersed in wood, which has become permeated with vegetative hyphae of the fungus'.

Ostiolate ascomata were commonly present in *Leptorhaphis* and many of its segregates. The position of this ostiole has been used in the past in the delimitation of families (Zahlbruckner, 1926), but such families are unnatural (Harris, 1975), and this feature can vary within a single genus. Lateral ostioles were observed in *Celothelium*, where this characteristic seemed to vary at species level, or within the same species as shown in vertical sections of *Leptorhaphis epidermidis*, where the ostiole was located either centrally or laterally; this may result from the inclination or aspect of the substratum. Some genera, such as *Rhytidiella* and *Lahmia*, open either by a more or less apical split or by a partial disintegration of the upper part of the wall respectively. The ascomata in the former consists of angular plates, and the split might occur at the junction of these. Eriksson (1981) called this schizolytic split-like ostiole a 'pseudostiole'.

Features of the wall such as thickness, colour, and tissue type (textura) have successfully been used at the specific level in wood- inhabiting discomycetes (Sherwood, 1977*a*). Peridial anatomy can prove to be important also at the family and order level in pyrenomycetes (e.g. Jensen, 1985), particularly surface views of the wall tissues. Reference to the terminology used here to describe the different types of textura can be found in Korf (1958). In surface view the majority of species accepted in *Leptorhaphis* showed a long-celled tissue with hyphae running in all directions with distinct interhyphal spaces (textura intricata), which occasionally have their walls united (textura epidermoidea). In vertical sections of *Cresporhaphis* and *Sarcopyrenia* this tissue is pseudoparenchymatous and consists of polyhedric cells without intercelullar spaces (textura angularis); in *Rhaphidicyrtis* this is composed of hyphae running more or less parallel and not cohering (textura porrecta).

In some genera of the Ostropales, the colour of the marginal tissues of the wall has been used to delimit groups of species at the generic level. This was the basis for segregating *Cyclostoma* from *Stictis* (Sherwood, 1977*a*). Another important characteristic in this group is the presence in *Stictis* of crystalline inclusions in the wall, whereas these were absent in *Odontura*.

Hamathecium

The nature of the interascal tissue (= hamathecium) present in the ascomata relates to its ontogeny (Hawksworth, 1985*a*). This neutral term was adopted by Eriksson (1981) 'to cover all kinds of hyphae or tissue between the asci or projecting into the locule or ostiole'. The different types of hamathecial elements summarized and illustrated by him are here fully accepted.

In earlier literature the terms paraphyses, pseudoparaphyses, and paraphysoids have been employed in different ways, and mistaken for one another, as reported by Luttrell (1965). However, Chesters (1938) already used the terms trabecular and cellular pseudoparaphyses in the sense used by Barr (1979) and accepted here. Theissen (1916; fide Luttrell, 1965) coined the term paraphysoids, but he used it in a broad sense covering both paraphysoids and pseudoparaphyses.

Leptorhaphis and other members of the Arthopyreniaceae (e.g. *Mycomicrothelia*; Hawksworth, 1985*a*) have anastomosing

and often branched, cellular pseudoparaphyses, about 1.5–2 μm broad, which 'originate from the hymenial cupola and grow downwards until finally becoming attached to the bottom of the ascomal cavity, and often become free in the upper part' (Eriksson, 1981). However, in a group of species studied here the hamathecium consists of trabeculate pseudoparaphyse (i.e. paraphysoids) presumed to originate by the 'stretching of the interascal or preascal tissue'; these can be differentiated from pseudoparaphyses in being narrower, about 1–1.5 μm, not or remotely septate, but also branched and anastomosed. This group of species is referred to a different genus partly on this basis, *Celothelium*, which is tentatively placed amongst the Pyrenulales.

Periphysate ostioles were observed in *Sarcopyrenia* and *Sagediopsis*, occurring with paraphyses and paraphysoids respectively. Eriksson (1981) reported that these may occur in ascomata with paraphyses, pseudoparaphyses or periphysoids, but did not report them in conjunction with paraphysoids. My observations of the interascal tissues within the perithecia of *Sagediopsis* revealed thin and anastomosing filaments apparently attached to the ascomal cavity at top and bottom.

Periphysoids were studied in single species of *Stictis* and *Odontura*. Young ascomata in these were superficially reminiscent of perithecioid ascomata, since the wall or exciple covered the hymenium. It is in these earlier stages that it is possible to observe short hyphae growing downwards, never reaching the base of the cavity. The wall breaks by the growth of the ascomata and carries the periphysoids to either side, which remain marginal subsequently.

Hymenial gelatin iodine reactions proved to be highly consistent at species and generic level by using Lugol's iodine on material pretreated with 10% KOH (Baral, 1987). This result was particularly useful as an additional character for the differentiation of the species in *Leptorhaphis*, and also in the rapid separation of the single species accepted in *Rhaphidicyrtis* (I+ deep blue) from those of *Celothelium* (I+ bluish-green), also with filiform and multiseptate ascospores.

Asci

Chadefaud (1973) regarded the shape of the ascus as useful in the diagnosis of certain groups, but as of secondary taxonomic importance, such as at family and generic level. Variations in ascus shape occur in *Leptorhaphis* s. lat., from cylindrical in *Celothelium*, cylindrical-clavate in *Leptorhaphis* s. str., to narrowly ovate in *Arthopyrenia*.

Luttrell (1951) divided the asci of the ascomycetes into 'bitunicate' and 'unitunicate' on the basis of differences in wall structure, and adopted a system of classification in which ascus structure was used as the primary criterion in dividing the Euascomycetes into two major series, the Bitunicate, equivalent to Nannfeldt's (1932) Ascoloculares, and the Unitunicate. In Luttrell's 'bitunicates', the ascus was 'surrounded by two separable walls, a relatively inextensible outer wall, or ectoascus, which ruptures at the apex to permit expansion of an extensible inner wall, or endoascus, to form a long tube through the apex of which the ascospores are forcibly discharged'. In his 'unitunicates', the ascus was 'surrounded by a single wall; uniformly thick or thickened at the apex and penetrated by a distinct pore'. He also concluded that these two types of ascus structure were correlated with a particular type of centrum development, as well as intimately associated with the mechanism of ascospore discharge.

Using stains, such as Iodine, Congo red, Chlorazol black, Janus green and black or blue-black Waterman's ink, Chadefaud (1973) showed that neither the outer wall ('exoascus') nor the inner wall ('endoascus') in the 'bitunicates' were single layered, and that 'unitunicates' were also composed of an 'exoascus' and an 'endoascus', which remained intimately attached, and towards the apex it was possible to distinguish an external layer of different composition from the 'exoascus'. These observations were later confirmed by his colleagues Parguey-Leduc (1977) and Parguey-Leduc & Janex-Favre (1982, 1984) using electron microscopic techniques. In spite of the multilayered construction of the 'bitunicate' ascus Müller (1981*a*) referred to the term 'bitunicate' as acceptable, and stressed the fact that both wall 'complexes' differ in their behaviour during ascospore ejaculation, a useful character to recognize 'bitunicate' asci in cases where two wall layers were difficult to observe.

Two or more wall layers are observed in many of the taxa previously referred to *Leptorhaphis*, but 'single' layered asci are present in *Cresporhaphis* and *Sarcopyrenia* and in the members of the Ostropales here discussed. In *Cresporhaphis*, this 'single' layered wall is uniformly thin, but on occasion becomes thicker at the apex and slightly indented by a pore, and the character is used in the differentiation of the species. In *Sarcopyrenia*, the wall is only observed in young asci, but becomes evanescent once the ascospores are mature.

The endoascus of *Leptorhaphis*, or 'endotunica' as it was termed by Eriksson (1981), shows an apical differentiation or internal apical beak, equivalent to what Chadefaud (1973) described as an apical 'nasse', and the morphology of this structure (broad and truncate or somewhat pointed) is used as an additional character to differentiate the species within the genus. The structure of this nasse was interpreted by Chadefaud (op. cit.) as consisting of four 'baguetes' longitudinally arranged, but the differentiation was not seen in my studies. In other groups, such as *Celothelium*, the apical beak is not observed. Instead, the ascus apex was capped by a meniscus, which became apparent in Congo red. A similar structure was described by Eriksson (1981) in the Acrocordiaceae, which suggests that both groups might be closely related within the Pyrenulales.

The structure and mechanisms by which asci open and discharge their spores are at present regarded as highly significant taxonomic criteria at the family level and above. However, Minter & Cannon (1984) found that in the Rhytismatiaceae, a family generally regarded as a natural group, a diversity of mechanisms of discharge occurred. This is not the case in *Leptorhaphis* where ascus discharge was only observed in fresh collections of *L. epidermidis*, and the mechanism was described as 'jack-in-the-box' or fissitunicate, as reported for *L. atomaria* (Ach.) Szat. and other members of the Arthopyreniaceae by Richardson & Morgan-Jones (1964). In the rest of the groups segregated from *Leptorhaphis* here, discharge was not observed. However, studies of empty asci of *Cresporhaphis muelleri* from herbarium material showed longitudinal creasing. Similar observations in asci of *Meloderma richeae*, a member of the Rhytismatiaceae, by Minter & Cannon (op. cit.), were interpreted as the ascus opening through a large split or circular hole.

Additional characteristics such as sequential ascus ripening and the production of multispored asci have been referred to in the literature (Minter & Cannon, 1984; Sherwood, 1981; Hawksworth, 1985*b*, 1987) as mechanisms of adaptation to particular environments, and therefore can arise by convergent evolution. Most of the taxa currently referred to

Leptorhaphis have sequential ascus ripening, and only *Odontura* and a single species of *Leptorhaphis* (*L. tremulae*) showed multispored asci. Polyspory arises by fragmentation in *Odontura*, whereas in *L. tremulae*, which has 16-spored asci, this is achieved pressumably by mitotic division after the initial 8-spore delimitation.

Ascospores

The morphology of the ascospores together with the appearance of the ascoma has been widely used in the differentiation of ascomycete genera, but colour, size, and shape of the spores, as reviewed by Sherwood (1981) and more recently by Hawksworth (1987), may be the result of functional adaptations to the environment and arise by convergence. This conclusion is supported by taxa referred to *Leptorhaphis*, which prove to contain many unrelated taxa placed together only on the basis of ascospore morphology.

The majority of the taxa included in *Leptorhaphis* have colourless narrowly fusiform ascospores with a homogeneous or vacuolar sporoplasm, and were grouped into generic units by the use of additional characters such as ascoma, hamathecium, and ascus structure. In the taxa retained in *Leptorhaphis*, the species were partly differentiated by the spore length: breadth ratio, septation, and morphology of the apices (i.e. attenuated or rounded). Some ascospores were very long, filiform and multiseptate, as in *Celothelium* and *Rhaphidicyrtis*, where each segment contains a few globose oil-like guttules, and a few were narrowly ovate or fusiform, as in *Arthopyrenia*. The ascospore shape in *Sarcopyrenia* can be described as remarkable, with bipolar symmetry, where the widest parts of the ascospore are at top and the bottom half (capitate ascospores). According to Hawksworth (1987), this shape tends to be correlated with active ascospore dispersal, functioning as a 'bolas'.

Evidence from ultrastructural studies shows ascospore walls to consist of three layers, which Eriksson (1981) termed 'endospore', 'epispore' and 'perispore'. However, the majority of the taxa included in *Leptorhaphis* have uniformly thin-walled ascospores, and none of these structures can be distinguished by light microscopy. An exception is the ascospores in some taxa referred to *Arthopyrenia*, with rather thick walls, that occasionally have a gelatinous sheath that becomes swollen and clear in KOH, or become pigmented and ornamented at maturity. Additional structures such as appendages were not observed in any of the taxa studied.

Eriksson (1967) regarded the sequence of ascospore septation as of considerable taxonomic value. However, in the ascospores of all the different groups studied here, septation is basically of the 'A-transsepta' type, where the two 'spore-halves' (= hemispores) are further divided by transsepta into equal segments.

Conidiomata

Müller (1981*b*) stressed that the delimitation of a species must be based on all available information, and therefore the same weight should be assigned to the anamorph as to the teleomorph. This information increases the possibility of a clear delimitation of fungal taxa, the testing of homogeneity in smaller or larger taxa, and relationship studies.

The investigation of the nature of the anamorph in lichen-forming ascomycetes has also been considered by Vobis & Hawksworth (1981) as of interest in separating taxa at higher taxonomic levels. However, the observation of these proved very difficult in *Leptorhaphis* and seggregated genera, due particularly to the small size of conidiogenous cells and conidia.

Pycnidial conidiomata varying in shape from somewhat conical to globose were observed in *Leptorhaphis*, *Arthopyrenia*, *Celothelium*, and *Cresporhaphis*, always opening through a central or more or less marginal ostiole, scattered amongst the ascomata, or as in *Celothelium* usually found at the margins of the thallus. Exceptionally *Celothelium stenobelum* has stromatic conidiomata (Fig. 40), where arcuate conidia are formed in a complex multilocular structure completely immersed in the matrix of host tissue, somewhat reminiscent of the structure resulting from the '*Xanthoria*-type' of conidial development described by Vobis & Hawksworth (op. cit.). Müller (1981*b*) believed that differences in the stromatic structure of the conidiomata, their presence or absence, and types of conidial anamorphs can be used in the differentiation of the genera, or in splitting a group into small genera. However, later in the same work he observed that this is only true when additional correlated data, such as differences in teleomorphs, or biochemistry, justify the splitting of such genera. On the basis of similar teleomorph characteristics, *Celothelium stenobelum* is consequently regarded as congeneric with the rest of the taxa in *Celothelium*.

Superficially, conidiomata are circular to ellipsoidal in most of the genera except *Celothelium*, where they adopt a more elongated shape. In vertical section wall structures and textura types similar to those in ascomata are also described.

The conidiogenous cells are always colourless, vary in shape from ampulliform to lageniform, and arise from colourless isodiametric cells adjacent to the conidiomatal wall, which can hardly been termed conidiophores since they are difficult to distinguish from wall cells. This type of conidiogenous cells were described by Vobis & Hawksworth (op. cit.) as 'type I'. They also believed that this type of conidiophores were very rare in lichen-forming fungi. However these structures were observed with much difficulty, and intermediate forms between type I and type II, or type II conidiophores sensu Vobis & Hawksworth might be present.

Another important taxonomic character, the conidiogenesis, was assessed with difficulty at the light microscope. The taxa are described as producing conidia enteroblastically, i.e. 'when the inner wall or neither wall of the blastic conidiogenous cell contributes to the formation of the blastoconidium (blastic conidium)' (Hawksworth et al., 1983). This type of conidiogenesis has also been described as phialidic, but terms such as 'phialide' or 'phialidic' were avoided since they are rather ambiguous and 'represent an attempt to sum up in one word a whole sequence of developmental events (conidial ontogeny, conidial secession ...)' (Minter et al., 1983). Electron microscopic studies of conidiogenesis have been carried out with success in both lichenized and non-lichenized taxa by using scanning and transmission techniques (Cole & Samson, 1979; Honnegger, 1984), and should become common practice in the investigation of conidial development.

Both types of conidia, microconidia and macroconidia, were found in *Leptorhaphis* and *Celothelium*, whereas in *Cresporhaphis* only microconidia were present. Microconidia were always colourless and thin-walled, and varied in shape from subglobose to bacilliform. Conidiomata bearing microconidia were abundant in the proximity of ascomata, and have been interpreted as functionally spermatial (Henssen &

Jahns, 1974; Müller, 1981*b*). Although the presence of macroconidia ('stylospores') have been scarcely reported in the literature (Henssen & Jahns, 1974; Harris, 1975; Hawksworth & Hill, 1984), these were found in combination with microconidia in *Leptorhaphis epidermidis* and on their own in a few species of *Celothelium*. In both examples the morphology of the conidia is reminiscent of the ascospore morphology, i.e. colourless, thin-walled and narrowly fusiform in *Leptorhaphis*, but very long, filiform and multiseptate in *Celothelium*. It is probable that these macroconidia act as propagules (Hawksworth & Hill, 1984).

The presence of anamorphs and other asexual propagules has been understood as a phenomenon influenced by adverse environmental conditions, and particularly associated with the ability to colonize ephemeral substrata (Bowler & Rundel, 1975; Sherwood, 1981). Conidiomata bearing macroconidia were found in species of *Leptorhaphis* and *Celothelium*, which may explain why they are characteristic of pioneer lichen communities.

BIOLOGICAL CONCEPTS

The diversity of fungal-algal associations can be accommodated in two major nutritional types: antagonistic interactions where 'the fungi involved take nutrients from the photobionts and eventually kill them' and mutualistic interactions where 'the fungus forms a stable association with the photobiont and neither partner is eliminated ... the fitness of both partners increases as a result of the interaction' (Hawksworth & Hill, 1984).

The different types of fungal-algal interactions have been summarized by Hawksworth (1988*a*,*b*). However, some associations traditionally studied by lichenologists have been difficult to categorize, and examples of this situation are found amongst the members of the Arthopyreniaceae, e.g. *Arthopyrenia* (Harris, 1975), *Mycomicrothelia* (Hawksworth, 1985*a*), and were also known in *Leptorhaphis* (Swinscow, 1965; Richardson, 1971). In these genera the fungal 'partner' is intimately associated with the bark tissues and probably obtains nutrients from the host. Exceptionally it shows small algal patches surrounding the ascomata, e.g. *Leptorhaphis lucida* and *L. deformis*, and were observed in vertical section even in old herbarium material. The nature of the algal 'partner' in these examples was difficult to elucidate since the algal cells had lost their pigmentation. On other occasions trentepohlioid algae were only seen in fresh collections, and in these species the fungus probably took advantage of this additional substratum. This was discussed by Sherwood (1981) for lignicolous fungi, where the wood also supports substantial populations of algae with which the fungi seem to be more or less associated. *Odontura* can be presented as an example, since on occasions green algae were found near the apothecia in vertical section and sometimes just below the hymenium and the exciple. However, *Odontura* is currently regarded as non-lichenized (Sherwood, 1977*b*; Sherwood-Pike 1987).

The biological implications of these examples were summarized by Hawksworth (1985*a*) for *Mycomicrothelia* as follows: never-lichenized species 'are generally extremely restricted with regard to their hosts, those in the intermediate category less, and certainly-lichenized species are probably not so host limited'. Aguirre & Hawksworth (1987) in preliminary studies of the genus *Leptorhaphis* also supported this view and gave several examples. *Leptorhaphis* is therefore regarded as a saprophytic fungus that may on occasion be associated with algal cells.

Since various taxa seemed to prefer a particular type of substratum, the morphological and anatomical variations by which the taxa were defined must have a genetic basis, and are not merely the result of the characteristics of the bark. For example, *Leptorhaphis atomaria*, *L. tremulae*, and *L. lucida*, are always found on *Populus* bark, but they vary in ascospore size, number of spores in each ascus, and hymenial iodine reactions. They also occupy different micro-habitats on the bark: *L. tremulae* is found mainly on branches, whereas *L. atomaria* and *L. lucida* are common on the trunk.

The remaining genera, *Celothelium*, *Cresporhaphis*, and *Rhaphidicyrtis*, are examples where algae are commonly found in association with the fungal component, and are regarded as lichenized. However, in these genera the fungal-algal interactions were not studied in detail.

TAXONOMIC RELATIONSHIPS

In recent years, and after a few attempts to incorporate lichens within an integrated system of fungal classification (Santesson, 1952, 1953, *fide* Hawksworth, 1985*b*), *Leptorhaphis* has been referred either to the Pleosporaceae (Poelt, 1974; Harris, 1975) or to the Arthopyreniaceae (Barr, 1977; Eriksson, 1981; Eriksson & Hawksworth, 1987*b*). Authors such as Luttrell (1973) and von Arx & Müller (1975), probably following Riedl (1962, 1963), did not recognize Arthopyreniaceae and referred *Leptorhaphis* to the Mycoporaceae as a genus composed of mainly tropical species. Von Arx & Müller (op. cit.) also found it very difficult to separate the Mycoporaceae from the Pleosporaceae.

However the main features of the family Arthopyreniaceae were synthesized by Barr (1979) and this group of fungi was defined as having applanate or deeply depressed ascocarps, peridium thickened at the sides and over the apex, with well differentiated clypeate tissues, and lacking hyphomycetous anamorphs characteristic of the Pleosporaceae. Furthermore Eriksson (1981) regarded Arthopyreniaceae and Mycoporaceae in separate clades, and distinguished both families primarily on the nature of the hamathecial tissues, i.e. pseudoparaphyses in Arthopyreniaceae and paraphysoids in Mycoporaceae. These views were accepted by Aguirre & Hawksworth (1987), when they referred *Leptorhaphis* to the Arthopyreniaceae, and are here further supported by the fact that all the species accepted in *Leptorhaphis* show a characteristic pseudoparaphysate hamathecium.

Species with paraphysoids in the hamathecium are referred elsewhere, e.g. *Celothelium*. The characteristic clypeate structure of the involucrellum in several species, e.g. *C. ischnobelum*, is to some extent reminiscent of the structure of the involucrellum in Arthopyreniaceae, although, this becomes carbonaceous and the shape of the asci, cylindrical, and the presence of paraphysoids in the hamathecium suggested affinities with the Trypetheliaceae. Moreover, a typical pseudostroma was observed in several species recognized in the genus (Fig. 28), as in members of the Trypetheliaceae (Johnson, 1959; Eriksson, 1981). However, IKI- rings were

not observed around the ocular chamber in any species of *Celothelium*; instead the asci seemed to be capped by a meniscus that became more apparent in Congo red preparations. A similar structure was described in the ascus apex of the Acrocordiaceae by Eriksson (op. cit.), but the ascospores in Celothelium do not have lenticular lumina as in many members of the Pyrenulales. Barr (1979) accepted many genera now in the Pyrenulales within the Didymosphaeriaceae (Melanommatales), but Eriksson & Hawksworth (1987*c*) did not support this view and placed both Didymosphaeriaceae and Melanommataceae in the Dothideales. A satisfactory systematic position has not yet been found for this genus, but it is provisionally referred here to the Pyrenulales.

Another taxon with hamathecium containing paraphysoids, *Rhaphidicyrtis*, is also tentatively referred to the Pyrenulales on the basis of ascomal anatomy. The ascoma was found to resemble that in *Porina byssophila*, studied in detail by Janex-Favre (1981), but this needs to be confirmed by comparative ontogenetic studies in the taxon. Furthermore the hymenial gelatin is blue in iodine and in *Rhaphidicyrtis* the ascus lacks a typical ring described by Harris (1975) for several members of the Trichotheliaceae.

Also with an uncertain position, the new genus *Cresporhaphis* is referred to the Trichosphaeriales on the basis of ascomata and ascus structure. The similarities between this group of taxa and some remaining species of *Zignoella* (Sacc.) Sacc. [i.e. *Zignoina* Cooke; Müller, *in* Eriksson & Hawksworth, 1987*b*] also support this view. These fungi with superficial, pyriform ascomata, hamathecium with paraphyses and occasionally periphysate, and thin ascus wall layers, were included by Keissler (1938) in a separate section of *Leptorhaphis*, sect. *Integrae*. The narrow apical ascus cap, slightly pierced by a pore in some species of the genus is somewhat reminiscent of the ascus apex illustrated by Sherwood & Boise (1986) for some species of *Xylopezia*. However, comparative studies of *Xylopezia hemisphaerica* (Fr.) Sherwood revealed a rather thick ectotunica in the asci, much thicker than in species of *Cresporhaphis*.

A few taxa referred to *Leptorhaphis* are found to belong to the genus *Sarcopyrenia* (Nyl.) Nyl. on the basis of ascoma and ascus structure and ascospore morphology. *Sarcopyrenia* has been traditionally accepted in the Verrucariaceae. Eriksson (1981) studied the ascus structure in various species of *Verrucaria*, and found that the endotunica was rather thick, and the ascus dehiscence was fissitunicate. However, my observations of the ascus morphology in *Sarcopyrenia* show that both ectotunica and endotunica are thin, deliquesce at an early stage, and presumably the discharge mechanism is not fissitunicate, as in the Verrucariaceae. Genera such as *Rhagadostoma* Körber and *Lasiosphaeriopsis* D. Hawks. & Sivanesan, accepted in the family Nitschkeaceae (Hawksworth, 1980; Eriksson & Santesson, 1986), also have stromatic ascomata, thin-walled asci, and periphyses in the ostiolar canal, and were considered as possibly related to *Sarcopyrenia*. However, Munk pores, characteristic of these genera, are not found in *Sarcopyrenia*. Consequently, the systematic position of this taxon still remains uncertain.

The remaining taxa are excluded from *Leptorhaphis* on the basis of similar criteria. Details of the taxonomy and systematic position for each particular case can be found below in the text.

KEY TO THE GENERA

This key includes the genera treated or discussed in this revision, stressing their main distinctive features. These sometimes belong to unrelated groups, with for example both 'bitunicate' or 'unitunicate' asci, and colourless, multiseptate, fusiform or filiform ascospores, but have in the past included species referred to the genus *Leptorhaphis* s. lat. Some of these genera are only provisionally referred here, since further critical studies, such as ontogenesis, need to be carried out for various taxa, where the taxonomic and systematic position still remains unclear. Additionally, a summary of the characteristics used to distinguish several genera which are discussed in more detail, is included in Table 1.

1. Asci with single functional wall layer, discharge not fissitunicate; hamathecium of paraphyses, or evanescent 2
– Asci with two functional wall layers, discharge fissitunicate; hamathecium of pseudoparaphyses or paraphysoids (trabeculate pseudoparaphyses) 6

2(1). Ascomata apothecioid, when young ± globose, soon becoming urceolate, opening by a pore; periphysoids leaning marginally; asci thin-walled, with a well differentiated apical cap, pierced by a conical pore; lignicolous 3
– Ascomata perithecioid, globose or flask-shaped, opening by a central ostiole; with periphyses, when present; asci uniformly thin-walled, sometimes with a narrow apical cap; saxicolous, corticolous or folicolous 4

3(2). Asci cylindrical, apical cap pierced by a pore, persistent at maturity, octosporous; ascospores multiseptate, not disarticulating at the septa; hymenial gelatin and asci bluish or unchanged in iodine; exciple with crystalline inclusions, textura intricata, becoming pseudoparenchymatous (textura angularis) in places ..... **Stictis**
– Asci cylindrical-clavate, apical cap only present in young asci, uniformly thin-walled at maturity, polysporous; ascospores multiseptate, disarticulating at the septa, producing 1-septate part-spores; hymenial gelatin and asci unchanged in iodine; exciple without crystalline inclusions, pseudoparenchymatous (± textura angularis) ..... **Odontura**

4(2). Ascomata usually ± immersed in the thallus, emergent, ± globose; ostiole located in a small depression or not; exciple parenchymatous (becoming a textura porrecta in places); asci uniformly thin-walled, truncate at the apex, with a refringent ring, never changing colour in iodine ..... **Porina**
– Ascomata superficial, flask-shaped, flat at the base; ostiole located in a small beak or papilla; exciple pseudoparenchymatous (textura angularis); asci not truncate, thin-walled, becoming thicker at the apex or not, without a refringent or amyloid ring 5

5(4). Exciple of two coloured layers; paraphyses persistent; ascospores fusiform, attenuated at the apices; corticolous ..... **Cresporhaphis**
– Exciple of three well differentiated layers; paraphyses deliquescing at maturity; ascospores cylindrical-capitate; saxicolous ..... **Sarcopyrenia**

6(1). Hamathecium of pseudoparaphyses; hymenial gelatin never deep blue in iodine 7
– Hamathecium of paraphysoids; hymenial gelatin blue or not in iodine 10

7(6). Ascomata superficial, hemispherical to subglobose, setose; involucrellum absent; exciple dark brown, pseudoparenchymatous (textura angularis) ..... **Capronia**
– Ascomata erumpent, applanate, ± mammiform; involucrellum

present, clypeate; without setae; exciple colourless, poorly differentiated, ± pseudoparenchymatous (textura angularis) 8

8(7). Involucrellum greenish-black, changing to deep green, later reddish-brown in HNO_3; ascospores broadly fusiform, attenuated at the apices ..... **Mycoglaena**
– Involucrellum dark brown to greenish-black, not changing colour in HNO_3; ascospores fusiform to narrowly ovate, attenuated or not at the apices 9

9(8). Asci cylindrical-clavate, apex broad and truncate; ascospores fusiform, attenuated at the apices, 0- to 5-septate ..... **Leptorhaphis**
– Asci cylindrical to narrowly ovate, apex often pierced by a narrow pore or dimple; ascospores narrowly ovate, 1-, 3-septate, cells somewhat unequal, apices rounded ..... **Arthopyrenia**

10(6). Ascomata immersed, only exposed in the ostiolar region, or erumpent, uni- or multilocular, ostiolate; lichenicolous or lichenized on bark 11
– Ascomata superficial, unilocular, non-ostiolate, opening by a split or partial disintegration of the upper part of the wall; saprobes or bark pathogens 13

11(10). Ascomata applanate, multilocular; ostiole marginally located in a small papilla; involucrellum always differentiated, carbonaceous; exciple, when present, reddish-brown, textura intricata, becoming pseudoparenchymatous in places ..... **Celothelium**
– Ascomata globose, unilocular; ostiole centrally located in a small depression; involucrellum ± differentiated; exciple well differentiated, dark brown, pseudoparenchymatous, textura porrecta in places 12

12(11). Involucrellum present, clypeate; ostiole not periphysate; hymenial gelatin I+ blue; ascospores filiform, multiseptate; lichenized (corticolous) ..... **Rhaphidicyrtis**
– Involucrellum absent; ostiole periphysate; hymenial gelatin not deep blue in iodine; ascospores fusiform, 3-, 5-septate; lichenicolous ..... **Sagediopsis**

13(10). Ascomata subglobose, mammiform; exciple pseudoparenchymatous (textura angularis) becoming carbonaceous towards the edges; paraphysoids always attached at both top and bottom; asci cylindrical; asci narrowly fusiform to filiform, multiseptate ..... **Rhytidiella**
– Ascomata turbinate or obpyriform; exciple composed of an hyphal net (textura intricata) with cells separated by a gelatinous substance; paraphysoids becoming free at the top, branched and swollen; asci clavate; ascospores not filiform 14

14(13). Ascomata turbinate; asci becoming loose in mature ascomata; free paraphysoids not forming an epithecium; ascospores fusiform-arcuate, rounded at the apices ..... **Lahmia**
– Ascomata obpyriform; asci and paraphysoids arranged in an hymenium covered by a thin epithecium formed by the branching apices of the paraphysoids; ascospores fusiform, attenuated at the apices ..... **Lahmiomyces**

I. **Leptorhaphis** Körber

Leptorhaphis Körber, *Syst. Lich. Germ.*: 371 (1855). *Arthopyrenia* sect. *Leptorhaphis* (Körber) Müll. Arg. in *Mém. Soc. phys. hist. nat. Genève* **16**: 430 (1862). *Verrucaria* subgen. *Leptorhaphis* (Körber) Harm. & Claud., *Guide Elem. Lich.*: 77 (1904). Type species: *Verrucaria oxyspora* Nyl. [*L. oxyspora* (Nyl.) Körber] (lectotype selected by Fries, 1861: 111). Nom. cons. over *Endophis* Norman (Lanjouw et al., 1956: 212).

Endophis Norman in *Nyt Mag. Naturvid.* **7**: 240 (1853). *Segestrella* sect. *Endophis* (Norman) Branth & Rostrup in *Bot. Tidsskr.* **3**: 258 (1869). Type species: *E. cerasi* Norman (holotype).

Sagedia [subgen.] *Campylacia* Massal., *Symm. Lich.*: 96 (1855). *Campylacia* (Massal.) Massal., *Sched. Crit.*: 184 (1856). *Arthopyrenia* sect. *Campylacia* (Massal.) Stizenb. in *Ber. tät. St. Gall. naturw. Ges.* **2**: 147 (1862) ['1860/61']. *Leptorhaphis* subgen. *Campylacia* (Massal.) Vainio in *Acta Soc. Fauna fl. Fenn.* **7**(2): 230 (1890). Type species: *Sagedia oleae* Massal. (lectotype selected here).

Sagedia Fink in *Contr. U.S. natn. Herb.* **14**: 235 (1910), non *Sagedia* Ach., *Lich. Univ.*: 327 (1810). Type species: *Sagedia oxyspora* (Nyl.) Tuck. (holotype); nom. illeg. (Art. 64.1).

Microthelia [sect.] *Atomariae* Jatta, *Fl. Ital. Crypt.* **3**: 897 (1911). Type species: *Microthelia atomaria* (Ach.) Körber (holotype).

Leptomycorhaphis Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittog. Pavia* V, **10**: 58 (1953). Type species: *L. oxysporae* (Nyl.) Cif. & Tom. (holotype); nom. illeg. (Arts 13.1(d), 63.1).

Leptorhaphiomyces Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittog. Pavia* V, **10**: 58 (1953). Type species: *L. maggianae* (Massal.) Cif. & Tom. (holotype).

Mycoleptorhaphis Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittog. Pavia* V, **10**: 58 (1953). Type species: *M. tremulae* (Körber) Cif. & Tom. (holotype).

Microtheliomyces Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittog. Pavia* V, **10**: 59 (1953). Type species: *M. atomaria* (Ach.) Cif. & Tom. (holotype).

Thallus: Absent or appearing whitish-grey to greenish, smooth, continuous, not well delimited; immersed in the substratum, composed of colourless, thin-walled hyphae, on occasion a few species are loosely associated with a trentepohlioid algae.

Ascomata: Perithecioid, reddish-brown, dark brown to black, smooth and shiny, scattered singly, sometimes confluent, circular to ellipsoidal; immersed in the substratum, becoming superficial, dimidiate, hemispherical to mammiform, ostiolate. Involucrellum: composed of dark brown to greenish-black, smooth, thin-walled, usually radiating hyphae, not changing colour in 10% KOH, intermixed with bark cells forming a clypeate tissue of textura epidermoidea to intricata, becoming pseudoparenchymatous with leptodermatous cells in some species; radiating hyphae extending beyond in a basal fringe, which can persist as a dark ring after the loss of the ascomata. Exciple: developed within the involucrellum, extending below the centrum in certain species, consisting of radially compresed pseudoparenchymatous, colourless to brown cells, textura angularis. Hamathecium: of pseudoparaphyses, composed of cellular, frequently septate, constricted at the septa, branched, anastomosing hyphae, forming a compact net enveloped in mucus; periphyses and periphysoids absent; hymenial gelatin orange or bluish-green, but never deep blue with iodine. Asci: arising from the base or angles of the ascomatal cavity, orientated towards the ostiole, ripening sequentially, cylindrical-clavate, short- and broad-stalked, with two functional wall layers, the outer layer thin and smooth, the inner thicker, especially at the apex, which can be broad and truncate, slightly indented, or more pointed; unchanged with iodine; discharge fissitunicate; 8-spored, or exceptionally 16-spored. Ascospores: arranged in

Table 1 Summary of characters separating the principal gerera previously referred to *Leptorhaphis* s.lat.

	Leptorhaphis	**Arthopyrenia**	**Celothelium**	**Cresporhaphis**	**Sarcopyrenia**	**Rhaphidicyrtis**
SYSTEMATIC POSITION:						
Order	Dothideales	Dothideales	Pyrenulales	Trichosphaeriales	Uncertain	?Pyrenulales
Family	Arthopyreniaceae	Arthopyreniaceae	Uncertain	Uncertain	Uncertain	Uncertain
ASCOMATA:						
Arrangement	individual	individual	individual to confluent	individual to confluent	individual	individual
Position	erumpent to superficial	erumpent	immersed to erumpent	superficial, except at the base	superficial, arising from thallus	erumpent, arising from thallus
Shape	applanate to hemispherical rarely mammiform, – dimidiate	applanate, rarely mammiform, – dimidiate	applanate to globose, sometimes dimidiate	flask-shaped, flat at the base, entire	conical-globose, flat at the base, complete	globose, complete
Involucrellum	clypeate, textura epidermoidea-intricata	clypeate, textura epidermoidea-intricata	clypeate	hyphal, textura angularis when present	—	clypeate
Exciple	hyphal, pseudo-parenchymatic	hyphal, pseudo-parenchymatic	hyphal, of textura intricata to pseudo-parenchymatic	hyphal, textura angularis to prismatica	hyphal, textura angularis	hyphal, pseudo-parenchymatic becoming textura porrecta in places
Colour	dark brown to greenish-black, unchanged with KOH	dark brown to greenish-black, sometimes olivaceous or greenish in KOH	reddish-brown to carbonaceous, unchanged	dark brown, unchanged with KOH	greenish-black, unchanged with KOH	dark brown, unchanged with KOH
HAMATHECIUM:	pseudoparaphyses	pseudoparaphyses	paraphysoids	paraphyses and periphyses	paraphyses soon evanescent, and periphyses	paraphysoids
Hymenial gelatin (I)	unchanged or bluish-green	unchanged or bluish-green	unchanged or bluish-green	unchanged or bluish-green	unchanged	blue
ASCI:						
Shape	cylindrical-clavate	cylindrical to ovate	cylindrical	cylindrical-clavate	cylindrical	cylindrical
Wall	multilayered	multilayered	multilayered	single-layered	single-layered	multilayered
Apex	broad and truncate, occasionally slightly pointed	narrow and pointed	rounded, capped by a meniscus	small cap pierced by conical or narrow pore	rounded, without differentiation	rounded, without differentiation
Discharge	fissitunicate	fissitunicate	?fissitunicate	non-fissitunicate	non-fissitunicate	not observed
ASCOSPORES:						
Shape	narrowly fusiform arcuate	fusiform to soleiform	filiform, sigmoid	narrowly fusiform, arcuate to sigmoid	capitate to fusiform, sigmoid	filiform, sigmoid
Septation	1- to 5-septate	1- to 3-septate	multiseptate	0- to 1- to 9-septate	0- to 1-septate	multiseptate
Colour	colourless	colourless to pale brown	colourless	colourless	colourless	colourless
Sheath	not developed	moderately to well-developed	not developed	not developed	not developed	not developed
CONIDIOMATA:	when known, pycnidial	pycnidial	pycnidial or stromatic	pycnidial	unknown	unknown
CONIDIA:						
Macroconidia	acicular-fusiform, arcuate, 0-1-, 3-septate	narrowly fusi- to soleiform, septate	very long and filiform, multi-septate	narrowly fusiform, arcuate, aseptate	unknown	unknown
Microconidia	bacilliform	bacilliform,	unknown	bacilliform	unknown	unknown
BIOLOGY:	saprophytic to loosely lichenized	saprophytic to loosely lichenized	lichenized: trentepohliod photobiont	lichenized (unknown chlorococcoid photobiont)	lichenicolous (presumably saprophytic)	lichenized (trentepohlioid photobiont)
NUMBER OF SPECIES:	12	*c.* 270	7	5	4	1
DISTRIBUTION:	N. Hemisphere, temperate-boreal	Cosmopolitan	N. & S. Hemisphere, temperate-tropical	N. temperate (Europe)	N. temperate	N. temperate

one or two bundles within the asci, each bundle consisting of ascospores arranged parallel to each other, sometimes twisted helically, acicular-fusiform, arcuate or sigmoid, distinctly pointed at one or both apices, colourless to pale brown, 1- to 5-septate, not constricted at the septa, thin and smooth-walled, lacking a gelatinous sheath or appendages.

Conidiomata: Pycnidial, black, shiny, circular to ellipsoidal, scattered between the ascomata; immersed to half-superficial, conical to subglobose, ostiolate. Wall: consisting of dark brown, thin-walled hyphae intermixed with bark cells forming a clypeate tissue, sometimes ± pseudoparenchymatous in places. Conidiogenous cells: ampulliform to lageniform, colourless, thin and smooth-walled, arising from colourless, isodiametric cells adjacent to the conidiomatal wall. Conidiogenesis: presumably enteroblastic. Macroconidia: colourless, acicular-fusiform, arcuate, thin-walled, smooth, somewhat similar in size to the ascospores, aseptate. Microconidia: colourless, bacilliform, thin-walled, smooth.

NUMBER OF SPECIES. Twelve species are accepted here, distinguished primarily by the size of ascomata and ascospores, ascospore septation, iodine reaction of the hymenial gelatin, presence of a basal fringe to the ascomata as a continuation of the involucrellum, and morphology of the ascus apex.

ECOLOGY. The majority of the European and North American species examined are saprobes on the bark of deciduous trees. They are characteristic components of pioneer fungal-lichen communities, and some prove to be almost exclusively host specific. Algal cells are occasionally seen on the surface of the bark near the ascomata in fresh collections. Exceptionally, proper differentiated thalli with intimate fungal-algal associations are observed on the surface and in vertical section as in *Leptorhaphis deformis*, *L. atomaria*, and *L. lucida*, where the fungal partner is associated with trentepohlioid algae.

DISTRIBUTION. Widespread in the boreal and temperate regions of Europe and North America, but probably overlooked due to their small size.

TYPIFICATION AND NOMENCLATURE. The generic name *Leptorhaphis* included two species when first introduced, *L. oxyspora* (Nyl.) Körber and *L. tremulae* Körber; the former was explicitly selected as the 'example' species of the genus by Fries (1861: 111), and this is accepted as an implicit lectotypification here. This name was accepted as the type of the genus in the list of *Nomina Generica Conservanda* in the Paris and subsequent codes (Lanjouw et al., 1956: 212) and in *Index Nominum Genericorum* (Farr et al., 1979: 968). Clements & Shear (1931: 288) mentioned *L. epidermidis* (Ach.) Th. Fr. as the type species, but this name was not accepted by Körber in the original account of the genus, since the name *Lichen epidermidis* Ach. [= *Verrucaria epidermidis* (Ach.) Ach.] had been misused for different species on smooth bark. Nevertheless, Fries (1860: 373) seemed to reject Körber's objections to the epithet '*epidermidis*' and recommended its use for the species, being an earlier name, and believing confusion would be avoided by the use of the generic name *Leptorhaphis* or *Campylacia*.

Leptorhaphis was first proposed for conservation over *Endophis* by Zahlbruckner (1935: 128), but was not formally accepted by the Special Committee for Lichen Nomenclature until the International Botanical Congress held in Paris in 1954 (Lanjouw et al., 1956: 212). However, in these references there is no mention of the type species of either genus, nor of the reasons for its conservation.

Campylacia was raised to the rank of genus by Massalongo (1856: 184). The name had been introduced in the previous year (Massalongo, 1855: 96) as a section or subgenus of *Sagedia* with an annotation in Italian of the diagnostic features of the new genus: 'Di rado si veggono i setti delle spore, e quasi le stimerei uniloculari, nel qual caso, falta regione anche alla strana morfologia degli apotecii, si dovrebbe creare il genere novello *Campylacia*'. This is sufficient for a diagnosis and the genus is therefore accepted as being validly published; *Sagedia oleae*, one of the first species included within the genus, and under which the note on the generic diagnostic characteristics of the genus was given, is selected as the lectotype here.

Sagedia Ach. (Acharius, 1810: 327) is typified by *S. depressa* Ach., which Fink (1910: 236) regarded as 'probably a *Pertusaria* or a *Verrucaria*'. Consequently he must be considered as having excluded the type and introduced a new generic name under Art. 72.1, based on the single species he included, i.e. *S. oxyspora* (Nyl.) Tuck.

The generic name *Spermatodium* Fée ex Trevisan was listed as a synonym of *Leptorhaphis* Körber by Eriksson & Hawksworth (1987*a*,*b*). The genus was introduced by Fée (1837: 49, 86) for various species with 'apotheciis simplicibus, nudis' and 'quatre spores concaténées', and later used by Trevisan (1860: 10), who also provided a more detailed generic description, and included as synonyms of *Spermatodium* the genera *Endophis* Norman, *Campylacia* Massal. and *Letorhaphis* Körber among others. Fée's small diagnosis is here accepted as a valid generic description of *Spermatodium*. The taxon *Verrucaria epidermidis* var. *albissima* Ach. [i.e. *Leptorhaphis epidermidis* (Ach.) Th. Fr.] was among the original species included by Fée in the genus, but it was described as the young stage of *Verrucaria cascarillae* Fée (1837: 86): 'La *Verrucaria epidermidis*, var. *albissima*, est traisemblablement la même plante que celle que nous décrivons, mais a l'état naissant'. Furthermore, *V. epidermidis* var. *albissima* is really the conidial state of *Leptorhaphis epidermidis* (Harris, 1973: 23), and since both Fée (1837) and Trevisan (1860) described the species in *Spermatodium* as having asci and ascospores, the taxon is not an appropriate choice as the lectotype of the genus, and this would be better selected from among the other taxa described within the genus, which are not related to *Leptorhaphis*.

Two further generic names were mentioned in Eriksson & Hawksworth (1987*a*) as possible synonyms of *Leptorhaphis*: *Arthopyreniomyces* Cif. & Tom. (1953: 57) and *Pyrenyllium* Clem. (1909: 41, 56). Both generic names are excluded from the synonymy above as they are based on *Lichen analeptus* Ach. [*Arthopyrenia analepta* (Ach.) Massal.], a name of uncertain application, which according to Harris (1975: 37) is a superfluous name for *Verrucaria olivacea* Pers. [= *Porina olivacea* (Pers.) A.L. Sm.], and strictly perhaps a species of *Baeomyces* (see Hawksworth, 1985*a*: 133).

RELATIONSHIPS. On the basis of ascomatal structure, hamathecial tissues, asci, and anamorphs, *Leptorhaphis* can be accommodated in the family Arthopyreniaceae Watson nom. cons. prop. (Hawksworth & Eriksson, 1988) of the order Dothideales (Eriksson, 1981: 29), together with *Arthopyrenia* Massal. s.str., and *Mycomicrothelia* Keissler (Hawksworth, 1985*a*) among other related genera. Other authors, such Harris (1973: 21) and Poelt (1974: 608), referred *Leptorhaphis*

to the Pleosporaceae and did not accept the family Arthopyreniaceae as such. Nevertheless, its ascomatal and asci structure, wall tissue and anamorph characteristics, also shared by the other genera now accepted in Arthopyreniaceae (Eriksson & Hawksworth, 1987*a*) are quite different from those of the fungi referred to the Pleosporaceae s.str., whose species have entire ascomata with no involucrellum, cylindrical asci, and hyphomycetous anamorphs (Eriksson, 1981).

Key to the species

1. Ascospores 3-, 5-septate; on trunks of *Olea* ..... 9. **L. oleae**
– Ascospores 1-, 3-septate 2

2(1). Ascomata ellipsoidal, surrounded by a dark basal fringe 3
– Ascomata circular, not surrounded by a dark basal fringe 5

3(2). Ascomata 180–300 µm; exciple not differentiated; ascospore length/breadth ratio 8–10: 1 ..... 1. **L. amygdali**
– Ascomata 300–450 µm; exciple always differentiated; ascospore length/breadth ratio 10–12: 1 4

4(3). Ascospores 25–35 × 2–3.5 µm; basal fringe less than 100 µm wide; hymenial gelatin orange amber in iodine; conidiomata always present, *c.* 100 µ diam; microconidia *c.* 4 × 1–1.5 µm; macroconidia *c.* 25 × 1.5–2 µm; on trunks and main branches of *Betula* ..... 5. **L. epidermidis**
– Ascospores 30–45 × 3–4 µm; basal fringe *c.* 170–300 µm; hymenial gelatin bluish in iodine; conidiomata not observed; on trunks of *Prunus* ..... 10. **L. parameca**

5(2). At least some ascospores 3-septate when mature 6
– Ascospores all 1-septate when mature 8

6(5). Hymenial gelatin yellowish in iodine; thallus inconspicuous; ascospores (25–) 30–45 × 1.5–2.5 µm, attenuated at the apices; conidiomata present, *c.* 100–150 µm; microconidia *c.* 3.75 × 1–1.5 µm; macroconidia 20–25 × 1–1.5 µm; on trunks of *Corylus* and *Quercus* ..... 8. **L. maggiana**
– Hymenial gelatin always bluish in iodine 7

7(6). Ascospores 35–40 (–55) × 2–3 µm, attenuated at the apices; thallus greenish-grey; on trunks of *Salix* and twigs of *Daphne* ..... 11. **L. psilotera**
– Ascospores (20–) 25–32 × 2–3.5 µm, rounded at the apices; thallus whitish-grey; on trunks of *Populus* ..... 2. **L. atomaria**

8(5). Hymenial gelatin bluish in iodine 9
– Hymenial gelatine not bluish in iodine 10

9(8). Ascospores 15–20 (–25) × 1.5–2 µm; thallus greenish grey; ascomata individual to confluent; asci 50–60 × 9–14 µm; conidiomata present, *c.* 100 µm; macroconidia *c.* 20–25 × 1 µm; on trunks of *Salix* and *Ilex* ..... 4. **L. deformis**
– Ascospores 30–40 (–47) × 2–2.5 µm; thallus absent; ascomata always individual; asci (35–) 45–55 × 18–17 µm; conidiomata absent; on twigs of *Larix* ..... 6. **L. laricis**

10(8). Ascomata 135–250 µm; ascospores 13–25.5 × 3–4.5 µm; asci 8–16-spored; on twigs and small branches of *Populus* ..... 12. **L. tremulae**
– Ascomata 300–350 (–500) µm; ascospores exceeding 25 µm in length; ascus always 8-spored 11

11(10). Ascospores 45–70 × 2.5–4 µm; thallus whitish-grey; ascus apex truncate; on trunks of *Populus* ..... 7. **L. lucida**
– Ascospores (25–) 30–45 × 1.5–2.5 µm; thallus absent; ascus apex slightly pointed; on twigs and trunks of *Betula* and trunks of *Quercus* ..... 3. **L. contorta**

The species

1. **Leptorhaphis amygdali** (Massal.) Zwackh in *Flora, Jena* **65**: 565 (1862). *Campylacia amygdali* Massal., *Sched. Critic.*: 184 (1856). *Leiophloea amygdali* (Massal.) Trevisan, *Conspec. Verruc.*: 9 (1860). *Verrucaria amygdali* (Massal.) Nyl. ex Zwackh, *Lich. exs.* no. 672 (1881); nom. inval. (Art. 29.1). *Sagedia amygadali* (Massal.) Jatta, *Monogr. lich. ital. meridion.*: 207 (1889). *Leptorhaphis parameca* f. *amygdali* (Massal.) Keissler, *Rabenh. Krypt, Fl.* **9** 1(2): 262 (1938). Type: Italy, Verona Province, on *Prunus amygdalus, A. B. Massalongo* [Massal. *Lich. Italic. exs.* no. 351] (BM!—lectotype, selected here, 2—isolectotypes; PAD—isolectotype).

Fig. 1, 2A.

Thallus: Absent.

Ascomata: Black, shiny, smooth, numerous, scattered singly, ellipsoidal, 180–300 µm diam, surrounded by a dark fringe; hemispherical to applanate, mammiform, 55–85 µm high; with a central ostiole located in a small depression. Involucrellum: greenish-black, *c.* 15–18 µm thick, extending beyond the ascomata in a long basal fringe, *c.* 80–240 µm in length; composed of bark material mixed with green-black, smooth, thin- walled hyphae, *c.* 4–5.5 µm, constricted at the septa and changing to reddish-brown with KOH + iodine, forming a clypeus of elongated radiating cells of textura intricata, becoming in places a pseudoparenchymatous tissue of leptodermatous cells. Exciple: not differentiated. Hamathecium: of pseudoparaphyses, *c.* 1.5–2 µm wide; hymenial gelatin bluish in iodine. Asci: clavate, somewhat ventricose, 42–65 × 13–19 µm, short and broad-stalked, usually curved; with two functional wall layers, the outer thin and smooth, the inner thicker, with a broad and truncate nasse, slightly indented; no other apical structures seen; 8-spored; discharge not observed, presumably fissitunicate. Ascospores: arranged in two bundles in the asci, colourless, thin-walled, smooth, fusiform, curvate, (25–) 30–38 × 3–4.5 µm, 1-septate, length/breadth ratio 8–10: 1, apices acute.

Conidiomata: Not observed.

ECOLOGY. On trunks of *Prunus amygdalus* Batsch [i.e. *Prunus dulcis* Miller & D.A. Webb]; presumably saprophytic.

DISTRIBUTION. Europe. Material has been seen from Italy and Germany. The species has probably spread to other areas where *Prunus dulcis* Miller & D.A. Webb is cultivated. Thus, Kondratyuk (1985) mentioned the species from USSR, in Latvian SSR, and Ukrainian SSR, as well as from Romania and Czechoslovakia. However, Moruzi et al. (1967) in their checklist of the lichens of Romania did not mention the species.

TYPIFICATION. I have been able to study four specimens of Massalongo's exs. no. 351 from BM and PAD distributed by the author; one of the specimens in BM is selected as a lectotype here since no material under this name could be located in Massalongo's herbarium in Verona (VER; F. Bianchini, in litt.).

OBSERVATIONS. Keissler (1938) remarked that Anzi's *Lich. Ital. super. exs.* no. 396 should be referred to *Arthopyrenia*, as *A. cerasi* Massal. Two specimens of this exsiccata collection have been studied in BM; this is a mixed collection, one of which does clearly belong to *Leptorhaphis amygdali*; but it is better to refer the second to *Arthopyrenia cerasi* Massal. as

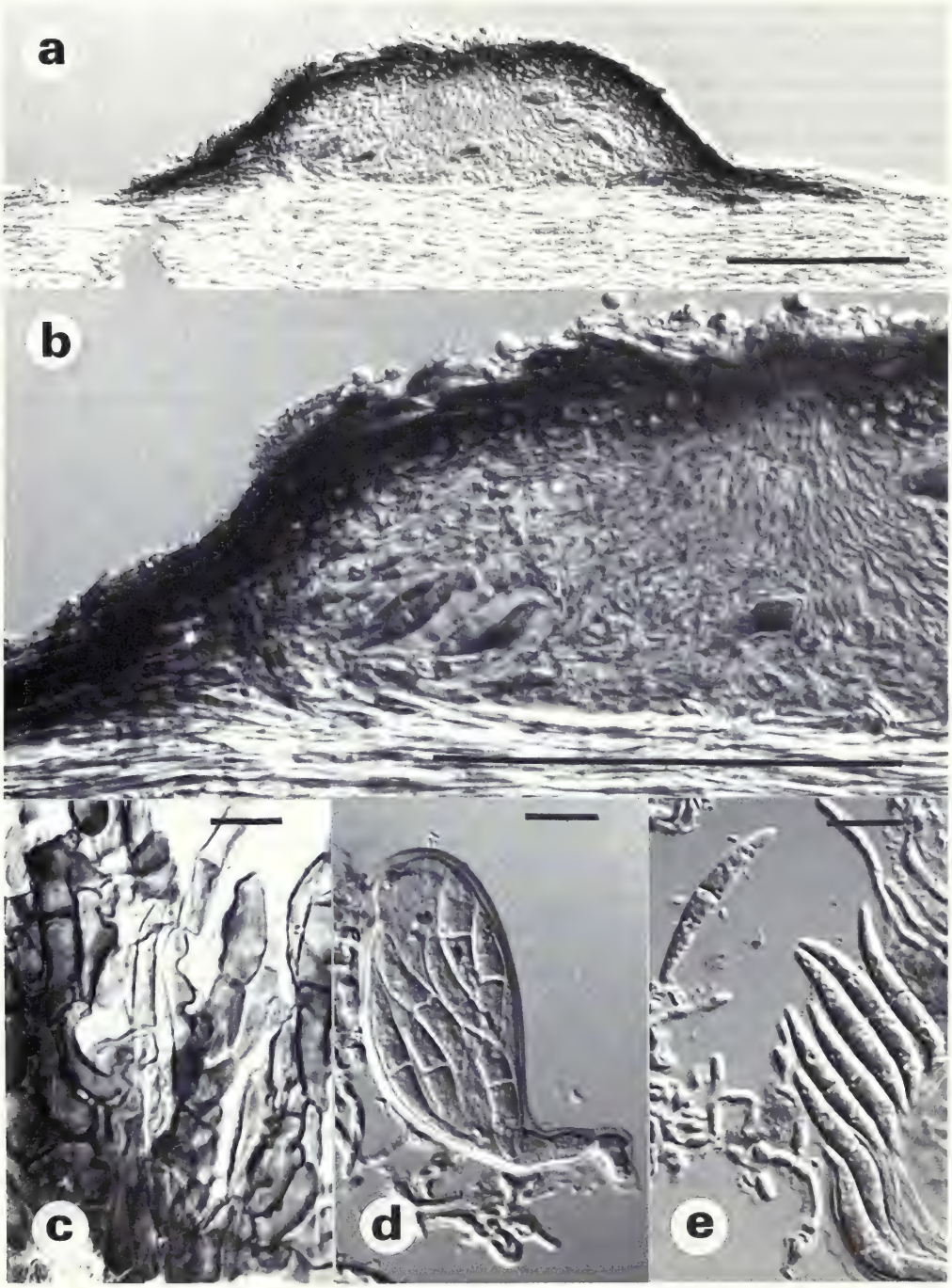


Fig. 1 *Leptorhaphis amygdali* (Massal.) Zwackh (BM–lectotype) (a) Vertical section of ascoma showing basal fringe; (b) Detail of involucrellum (in vertical section) showing clypeus; scale = 100 μm; (c) Detail of involucrellum (surface view): textura epidermoidea; (d) Ascus and ascospores; (e) Ascospores; scale = 10 μm.

Keissler suggested, since it has 4-celled, soleiform ascospores. This species differs from *L. parameca*, which also occurs on *Prunus*, in the larger ascospores (30–42.5 × 3–4 μm), which also have a much larger length: breadth ratio.

Although conidiomata were not observed in the collections examined, Harris (in litt.) found macroconidia similar to ascospores, *c.* 15–19 × 1.5–3 μm, 0-, 1-, possibly 3- septate, and bacilliform microconidia, *c.* 4 × 0.8 μm in Massalongo's *Lich. Italic. exs.* no. 351 from NY.

ADDITIONAL SPECIMENS. **Germany**, Baden-Württemberg, Heidelberg, 'in der Weinbergen des rechten Necharnfers', on *Prunus dulcis*, 28 March 1881, *W. R. von H. Zwackh* [Zwackh, *Lichenes exs.* no. 672, as *Verrucaria amygdali*] (PC HUE

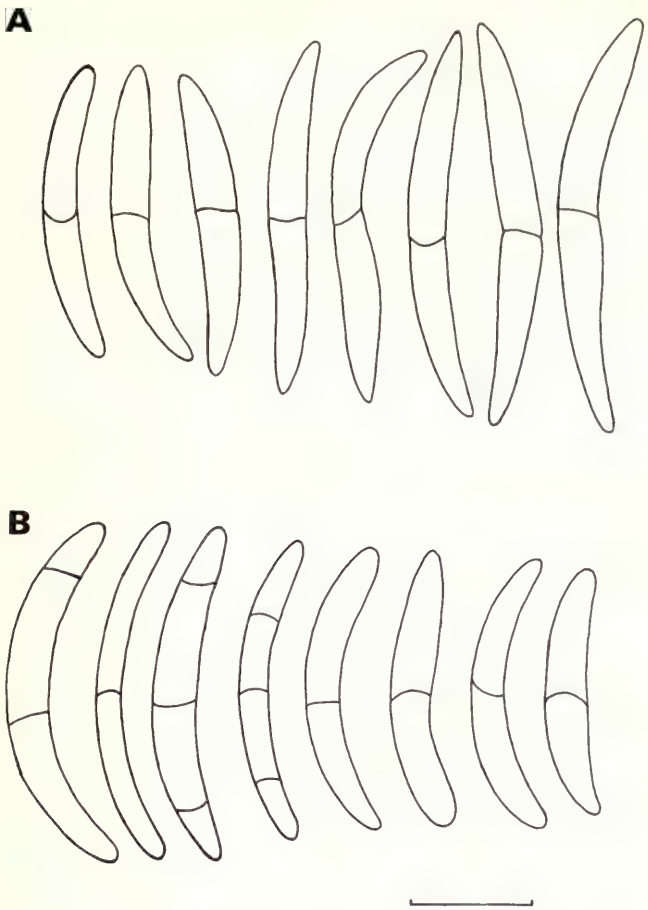


Fig. 2 Ascospore outlines (A) *Leptorhaphis amygdali* (Massal.) Zwackh (PAD–isolectotype); (B) *Leptorhaphis atomaria* (Ach.) Szat. (H-ACH 795a–lectotype); scale = 10 µm.

3505/5, B 59630, 59712). **Italy**, Verona Province, *Prunus amygdalus*, *A. B. Massalongo* [Anzi, *Lich. Ital. supl. exs.* no. 396, as *Sagedia amygdali*] (BM).

2. **Leptorhaphis atomaria** (Ach.) Szat. in *Magy. bot. Lap.* **26**: 31 (1928). *Lichen atomarius* Ach., *Lich. Suec. Prod.*: 16 (1798). *Verrucaria stigmatella* var. *atomaria* (Ach.) Ach., *Method. Lich.*: 117 (1803). *Verrucaria punctiformis* var. *atomaria* (Ach.) Ach., *Synops. Lich.*: 87 (1814). *Verrucaria atomaria* (Ach.) DC *in* Lamarck & De Candolle, *Fl. Fr. franç.*, 3rd ed., **2**: 313 (1805). *Verrucaria epidermidis* var. *atomaria* (Ach.) Schaerer, *Lich. Helvet. Spicil.* sect. 7: 344 (1836). *Microthelia atomaria* (Ach.) Körber, *Syst. Lich. Germ.* : 373 (1855). *Arthopyrenia persoonii* f. *atomaria* (Ach.) Massal., *Sched. Critic.* **8**: 143 (1856). *Pyrenula punctiformis* var. *atomaria* (Ach.) Hepp, *Flecht. Europ.*, no. 456 (1857). *Arthopyrenia punctiformis* var. *atomaria* (Ach.) Anzi, *Catal. Lich. Sondr.*: 108 (1860). *Leiophloea punctiformis* var. *atomaria* (Ach.) Trevisan, *Conspec. Verruc.*: 9 (1860). *Tichothecium atomarium* (Ach.) Krempelh. in *Denkschr. Bayer. bot. Ges. Regensburg* **4**: 299 (1861). *Arthopyrenia epidermidis* var. *atomaria* (Ach.) Mudd, *Manual Brit. Lich.*: 305 (1861). *Arthopyrenia atomaria* (Ach.) Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **16**: 429 (1862). *Verrucaria epidermidis* var. *analepta* f. *atomaria* (Ach.) Malbr. in *Bull. Soc. Amis Scienc. Nat. Rouen* **5**: 314 (1869). *Didymosphaeria atomaria* (Ach.) Rehm *in* Sacc., *Syll. Fung.* **1**: 715 (1882). *Arthopyrenia analepta* var. *atomaria* (Ach.) Jatta, *Syll. Lich. Ital.*: 527 (1900). *Campylacia atomaria* (Ach.) Vainio in *Acta Soc. Fauna Flora fenn.* **49**(2): 189 (1921). *Didymella atomaria* (Ach.) Szat. in *Botan. Közlemeny.* **27**: 5 (1930). *Mycomicrothelia atomaria* (Ach.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1(2): 33 (1936). *Microtheliomyces atomariae* (Ach.) Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittogam. Pavia* V, **10**: 59 (1953). Type: Sweden, on *Fraxinus* (H ACH 795a!—lectotype).

?*Sagedia salicis* Massal., *Symm. lich.*: 97 (1855). Type: Italy, 'ad truncos *Salicis* in Prov. Patavina extra urbis moenia', *L. F. Beltramini* (not located).

Microthelia adspersa Körber, *Lich. sel. Germ. exs.* no. 326 (1868); nom. inval. (Art. 32.1). *Microthelia adspersa* Körber ex Stein *in* Cohn, *Krypt,Fl. Schles.* **2**(2): 332 (1879). Type: Poland, Silesia, Hirschbergam, Sattler wood, on bark of *Populus tremula*, *G.W. Körber* [Körber, *Lich. sel. Germ. exs.* no. 326] (WRSL!—lectotype, selected here; L!—isolectotype).

?*Verrucaria populicola* Nyl. in *Not. Sällsk. Fauna Flora fenn. Förhandl.* **13**: 344 (1873); nom. inval. (Art. 32.1); Nyl ex Vainio in *Meddn Soc. Fauna Flora fenn.* **10**: 188 (1883). Type: Findland, '... in Karelia boreali et regione infralapponica Ostrobotniae. In regione pinifera Lapponiae Inarensis: ad Ruoptuinvaara; in regione betulina: ad Köngäs prope Mare glaciale. Ad corticem praesertim populi vel etiam salicis obvia' (Not seen).

Leptorhaphis tremulicola Havaas, *Lich. Norvegiae* exs. no. 106 (1900); nom. inval. (Art.29.1). Type: Norway, Granvin, Hardanger, 340m, on *Populus tremula*, 16 March 1900, *J. J. Havaas* [Havaas, *Lich. Norvegiae exs.* no. 106] (O!—holotype).

Fig. 2B, 3.

Thallus: Smooth, whitish, very thin, continuous and not well delimited; immersed in the substratum, composed of colourless to greenish-brown, smooth-walled hyphae, *c.* 3 µm wide, constricted at the septa; associated with trentepohlioid algae, filaments *c.* 10 µm wide.

Ascomata: Black, matt, smooth, scattered singly, numerous, circular, with a small dark fringe remaining when the perithecia disappears, 130–150 (–200) µm diam; superficial, hemispherical, applanate, *c.* 90–110 µm high, dimidiate or not; with a centrally located ostiole. Involucrellum: greenish-brown, *c.* 15.5–20 µm thick, sometimes extending beyond the ascomata to form a short fringe up to 30 µm long; composed of bark material, mixed with greenish-black, smooth, thick-walled, isodiametric cells, with enlarged lumina, *c.* 4.5–5.5 µm wide, forming a pseudoparenchymatous tissue of leptodermatous cells. Exciple: surrounding completely and usually continuing below the centrum, colourless to pale brown, *c.* 9–18 µm thick; composed of colourless to dark brown, smooth, thin-walled, radially compressed isodiametric cells with enlarged lumina, individually *c.* 3–4 µm diam, forming a pseudoparenchymatic tissue of leptodermatous cells at both base and sides of the ascomata cavity. Hamathecium: of pseudoparaphyses, *c.* 2–2.5 µm wide; hymenial gelatin bluish in iodine. Asci: clavate, short and broad-stalked, (35–) 40–55 × 10–15 µm, sometimes slightly curved; with two functional layers, the outer thin and smooth, the inner thicker, especially at the

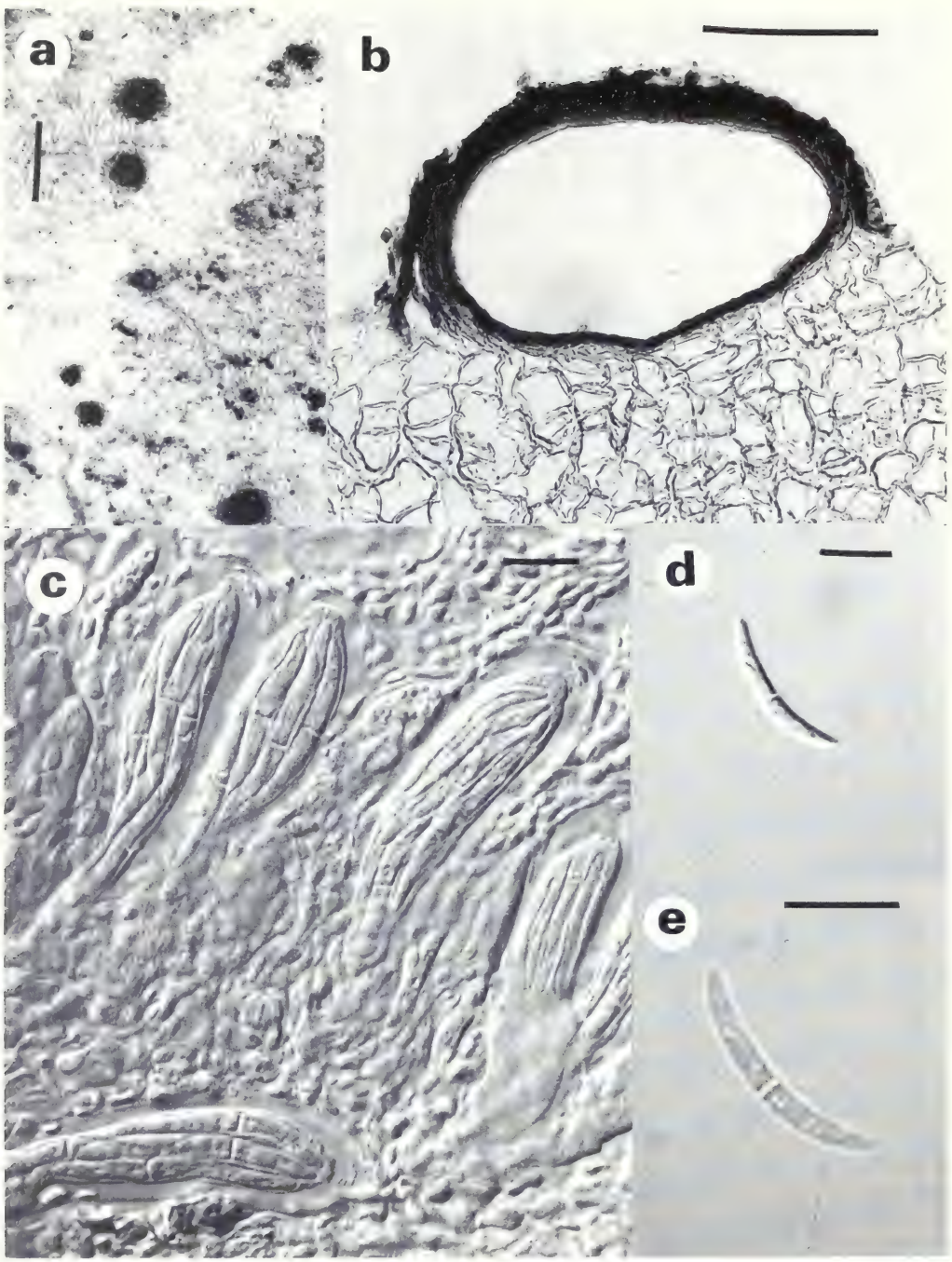


Fig. 3 *Leptorhaphis atomaria* (Ach.) Szat. (H-ACH 795a–lectotype) (a) Surface view of ascomata; scale = 500 μm; (b) Vertical section of ascoma, showing exciple extending below ascoma; scale = 100 μm; (c) Asci, ascospores and pseudoparaphyses; (d), (e) Ascospores; scale = 10 μm.

apex, which is broad and truncate; 6-, 8-spored. Ascospores: arranged in two bundles in the asci, filiform, curvate, sometimes sigmoid, (20–) 25–32 × 2–3.5 μm, 1-, 3-septate, somewhat rounded apices.

Conidiomata: Pycnidial, smooth, blackish, numerous, scattered singly among the ascomata, *c.* 100–160 μm diam; immersed in the bark, becoming superficial, globose, ostiolate. Wall: composed of dark brown, thick-walled, isodiametric cells with enlarged lumina, *c.* 6–9 μm diam, forming a textura globulosa. Conidiogenous cells: colourless, smooth, thin-walled, lageniform cells, not branching *c.* 11.5 × 1.5–2.5 μm, arising from colourless, isodiametric cells, *c.* 2.3–3.5 μm diam, adjacent to the conidiomatal wall. Conidiogenesis: probably enteroblastic. Macroconidia: colourless, narrowly fusiform, arcuate, aseptate, *c.* (11.5–) 16.5–18 × 1.5–2.5 μm.

ECOLOGY. On bark of *Fraxinus excelsior* L. and particularly on species of *Populus*, growing on the trunk, often mixed with lichens such as *Xanthoria parietina* (L.) Th. Fr. and species of *Caloplaca* and *Lecanora*; perhaps facultatively lichenized with trentepohlioid algae or not.

DISTRIBUTION. Widespread in temperate regions of Europe, it has also been mentioned from Northern America (Harris, 1973: 22).

TYPIFICATION. The lectotypification of *Lichen atomarius* Ach. by Vainio (1921: 189) was accepted also by Harris (1973: 22) on the basis of Acharius' description of the locality and nature of the substratum. Thus, the specimen selected from the Acharian collection under the name of *Verrucaria atomaria* in H ACH 795, was collected in Sweden, probably on *Fraxinus* bark, as stated by Vainio (op. cit.). This lectotypification is also accepted here.

A source of confusion has been the concurrent misapplication of the epithet *atomaria* for a *Mycomicrothelia* species, *M. melanospora* (Hepp) D. Hawksw. (Hawksworth, 1982: 134; Hawksworth, 1985*a*: 98, 135). Körber (1855), able to recognize the confusion, believed that this probably originated in the misinterpretation of De Candolle's species *Verrucaria atomaria*, which formed white patches on the bark of ash and poplar (Lamark & De Candolle, 1805: 311). Nevertheless De Candolle did not pretend to introduce a new taxon, but applied Acharius' epithet as he stated in the same work: '*Lichen atomarius*. Ach. Lich. 16'.

According to Hawksworth (1985*a*: 130) the taxon *Microthelia adspersa* Körber ex B. Stein should be typified by Korber's exsiccate, since the name was validated by B. Stein (in Cohn, 1879, fide Hawksworth, 1985*a*), and he based the description on the exsiccate material. Therefore, a specimen from B. Stein's herbarium at WRSL, part of the exsiccate collection no. 326, is here selected as the lectotype.

OBSERVATIONS. The study of several examples of Körber's *Lich. sel. ger. exs.* no. 326 (sub *Microthelia adspersa*), and additional collections, which included a specimen from Körber 'typenherbar' at L, supports Keissler's (1937: 256) and Hawksworth's (1985*a*: 130) opinions that the taxon should be referred to *Leptorhaphis atomaria* (Ach.) Szat., since the species has colourless, falcate, 1-, 3-septate ascospores. However, a specimen collected in 1863, also from Sattler Wood, in WRSL was found to be closely related to a *Mycomicrothelia* species on the basis of its reddish-brown, soleiform and verrucose ascospores (Fig. 4). It seems that after all, Körber intended to describe a '*Microthelia*' species, but distributed a different taxon in his exsiccate. On the basis of the lectotypification above accepted, the name must be placed as a synonym of *Leptorhaphis atomaria*.

Sagedia salicis was described by Massalongo (1855: 97) for a species of similar characteristics to *Leptorhaphis atomaria*, collected on *Salix* bark by L. F. Beltramini, but the type material was not located in VER and PAD. Later Massalongo (1856: 184) renamed the species *Campylacia tremulae* (Körber) Massal., and also distributed material as *Lich. Ital exs.* no. 352, which proved to be similar to *L. atomaria*.

Nylander (1873: 344) introduced the name *Verrucaria populicola* without a proper description; thus the name is invalidated by Art. 32.1. Some years later Vainio (1883: 188) produced a description for the species, general features of which, such as whitish thallus, fusiform-acicular, 3-septate ascospores (16–30 × 3–4 μm) resemble those of *Leptorhaphis atomaria*. I have not been able to study type material of this species, but Vainio's full and detailed description of the taxon is sufficient to include it as a synonym of *L. atomaria*.

Leptorhaphis atomaria has been repeatedly mistaken for *L. tremulae*, also on *Populus* bark. This confusion presumably originated in Körber's description of *L. tremulae*, which does not totally agree with the specimen regarded here as the lectotype (p. 00), with polysporous asci, lack of thallus and iodine reaction, and slightly smaller ascospore size, but it was more closely related to *L. atomaria*. Later, this interpretation was assumed by Vainio (1921: 189), when he lectotypified both taxa with *Lichen atomarius*.

North American collections of *Leptorhaphis atomaria* studied by Harris (1973: 22), mainly gave an orange iodine reaction, and only occasionally a pale bluish one. My studies of European material of the species showed that in Lugol's iodine, pretreated with 10% KOH, the converse was true; most were I+ pale bluish.

Two other species are known to occur on *Populus* bark, *L. lucida* and *L. tremulae*, which can be separated by the features presented in Table 2.

Table 2

	L.atomaria	*L. lucida*	*L. tremulae*
Thallus	whitish-grey	whitish-grey	inconspicuous
Ascomatal size	130–150 (–200) μm	300–500 μm	135–250 μm
Hymenial gelatin	I+ bluish	I-, or amber	I-, or amber
Asci	(35–) 40–55 × 10–15 μm; 8-spored	60–73.5 × 10.5–15 μm; 8-spored	40–60 × 18–25 μm 8-, 16-spored
Ascospores	(20–) 25–32 × 2–3.5 μm; rounded apices	45–65 (–70) × 2.5–4 μm; attenuated at the apices	13–25.5 × 3–4.5 μm; rounded apices
Ecology	on trunks of *Populus* spp.	on trunks of *Populus* spp.	on twigs and branches of *Populus* spp.

Although microconidia were not observed, Harris (in litt.) found in a specimen from Ontario (Canada) kept at NY that these are bacilliform, *c.* 4 × 0.8 μm.

ADDITIONAL SELECTED SPECIMENS. **Austria**, Lechtaler Alper, Lech Tal Valley, 'Höhenzug', on *Populus* (B 59631). **British Isles**, Scotland, South Aberdeen, Braemar, Chinnie Water, near tennis courts, on boles of mature poplar, May 1964, P. W. James (BM). Forfar, Montrose, opposite Charleton Maternity Hospital, 28 November 1966, *P. W. James* (BM). Easterness, Aviemore, Loch an Eilein, with *Lecanora pallida* on *Populus tremula*, 3 August 1968, *P. W. James* (BM). Ayrshire, Ness Glen, Dalmellington, 5 August 1975, *B. J. Coppins* 909 (BM, E). Glen Cannich, by River Cannich, SW. of Muchrachd, *c.* 180 m, on *Populus*, 22 June 1976, *B.J. Coppins* 3232 (E). Wales, Dyffed, St. Davids, Whitchurch, near Solva, *c.* 290 m, on twigs of young Lombardy Poplar growing in a disused hen-run with *Sambucus nigra* covered with *Lecanora sambuci* (BM). **Czechoslovakia**, Presov ['Eperies'], *F. A. Hazslinsky* (BM). **Finland**, Tavastia australis, Asikkala, Kaila, 'ad corticem *Populi tremulae*', 1873, *J. P. Norrlin* [Nylander & Norrlin, *Herbarium Lichenum*

Fig. 4 *'Microthelia' adspersa* Körber (WRSL) (a) General view of packet; (b) Surface view of ascomata; scale = 500 μm; (c) Detail of exciple: textura angularis; (d) Ascus and ascospores; (e) Ascospores; scale = 10 μm.

Fenniae exs. no. 802, as *Campylacia atomaria*] (BM). Helsinki, 'Helsingforsia, ad corticem *Populi tremulae* in silva', 18 October 1880, *J. P. Norrlin* [Nylander & Norrlin, *Herbarium Lichenum Fenniae exs.* no. 803, as *Campylacia atomaria*] (BM). Tavastia borealis, Saarijärvi, Mahlu, Kitka, 'ad corticem *Populi tremulae*', 16 June 1941, *A. Koskinen* [Räsänen, *Lichenes Fenniae exs.* no. 998, as *Campylacia atomaria*] (BM). **France**, Brittany, Finistère, Contadon, 'sur le talle du *Lecanora subfusca*, sur un Pouplier noir', 20 October 1868, *P. L. & H. M. Crouan* (Concarneau). Normandy, Manche, Canisy, Le Hardichon, 'sur un *Populus nigra*', September 1888 (PC-HUE 3505/1). **East Germany**, Schwerin, 'auf jüngen Zugpappeln?', September 1844, *Würtnei* (B 59714). **West Germany**, Nordrhein-Westfalen, Greven, near Münster, on *Populus*, September 1859, *W. Fuisting* (B 59593). Höxter, Rothegrund, on *Populus tremula*, April 1874, *K. Beckhaus* (B 59592). Saarland, near Cranz, Waldhaus, on *Populus tremula*, 20 August 1902, *G. Lettau* (B 59711). **Italy**, Badia,

on *Salix* and *Populus*, *A. B. Massalongo* [Rabenhorst, *Lich. europaei exs.* no. 147, as *Campylacia tremulae*] (BM—2 specimens). Novo-Comensi Province, 'ad corticem populorum' [Anzi, *Lich. Langob. exs.* no. 521, as *Sagedia (Campylacia) tremulae*] (BM, PC). [Sine loc.], *A. B. Massalongo* [Massalongo, *Lich. Italiae exs.* no. 352, as *Campylacia tremulae*] (BM—4 specimens, PAD). Vicenza, on bark of *Populus tremula*, 1870, *V. Trevisan [Erbar. Crittogam. Ital. II exs.* no. 371, as *Campylacia tremulae*] (BM). Oliero, 'Bassanensi', on bark of *Populus* [Trevisan, *Lichenotheca veneta, I (II) exs.* no. 51, as *Spermatodium tremulae*] (BM). Tuscany, Lucca Province, east of Bagni di Lucca, Fabbriche, east side of the village, mixed deciduous woodland, on *Populus*, 27 April 1985, *B. J. Coppins, P. W. James & F. Rose* 12306 (E). **Norway**, Leko Island, 29 June 1880, *J. M. Norman* (O). Akershus, Asker paroch., between Asker and Ravnsborg, *J. M. Norman* (O). Oslo, Ryenberget, 26 April 1868, *N. G. Moe* (O). Tavern paroch., Norderhov, *J. M. Norman* (O). Vestfold, Larvik, Jordfalden, on *Populus* bark, *J. M. Norman* (O). Finnmark, Karasjok, Arrebakle, 1866, *J. M. Norman* (O). Gyfjord, Seiland, *J. M. Norman* (O). Achen, 'Lerbebhen', Tverelodal, *J. M. Norman* (O). Balesfjord, 'Mipe junla Sagvaad', *J. M. Norman* (O). Moer, 'Moerl selven', on *Populus*, 1865, *J. M. Norman* (O). Bardor, Rabben, on *Populus*, 1868, *J. M. Norman* (O). Skjervó, Reisen, on *Populus*, 1865, *J. M. Norman* (O). Nordland, Bejeren, 'Keminghgh', *J. M. Norman* (O). Rödöy ['Rådo'] Island, 13 June 1876, *J. M. Norman* (O). Nesna, Tomma, Finvika, on *Populus tremula*, 'pa basen ar asp', 14 August 1970, *O. Eriksson* (Umeå 29068). **Poland**, Silesia, Hirschbergam, Sattler Wood, *G. W. Körber* (L Körber typenherbar, WRSL). Wroclaw, Coseler wood, on *Populus tremula*, 3 January 1871, *B. Stein* (WRSL, L). Sweden, Hålland, Lindome paroch., Inseråsa, on the trunk of *Populus tremula*, 28 February 1933, *A. H. Magnusson [Magnusson, Lich. sel. scandinavici exs.* no. 126, as *Campylacia atomaria*] (BM). Närken ['Nerikes'], *P. J. Hellbom* (BM). Götlunda, Visby, on *Populus*, August 1910, *E. P. Vrang* (B 59717). **Switzerland**, Zürich, 'auf Zitterpappeln bei Uerzlikon?', 1880, *C. Hegetschweiler* (B 59686).

3. **Leptorhaphis contorta** Degelius in *Ark. Bot.* **30**: 13 (1942). Type: USA, Maine, Prince's Point, near Brunswick, Arcadia Inn, on *Quercus rubra* in mixed wood, 3 September 1939, *G. Degelius* (herb. Degelius!—holotype; US—isotype)

Fig. 5, 6A.

Thallus: Inconspicuous; fungal hyphae in connection with trentepohlioid algae are seen in vertical section in the proximity of the ascomata, on the surface or immersed in the substratum.

Ascomata: Black, shiny, smooth, circular to ellipsoidal, not surrounded by a basal fringe, scattered singly, *c.* 300–450 µm diam; immersed in the substratum becoming superficial, hemispherical to applanate, dimidiate, *c.* 70–85 µm high; ostiole centrally located in a small depression. Involucrellum: dark brown to greenish-black, *c.* 20–30 µm thick, covering the exciple except at its base, not extending beyond in a basal fringe; consisting of brown to greenish-black, smooth, thin-walled hyphae, *c.* 3 µm wide, intermixed with bark material, forming a clypeus of textura epidermoidea-intricata, becoming in places a pseudoparenchymatous tissue of leptodermatous cells. Exciple: colourless to pale brown, thinner than the involucrellum and intergrading with it; composed of colourless, thin-walled and isodiametric cells, forming a textura angularis. Hamathecium: of pseudoraphyses, 2–2.5 µm wide; hymenial gelatin yellowish-green in iodine. Asci: clavate, short- and broad-stalked, *c.* 45–60 × 10–13.5 µm, with two functional layers, the inner wall thicker at the tip, with a broad and slightly pointed apex; 8-spored. Ascospores: arranged in two bundles within the asci, fusiform, arcuate to sigmoid, (25–) 30–45 × 1.5–2.5 µm, 1-septate, attenuated at the apices.

Conidiomata: Not observed.

ECOLOGY. On bark of *Quercus rubra* du Roi [i.e. *Q. borealis* Michx.] and twigs and trunks of *Betula*; saprobe, not causing any apparent damage; occasionally trentepohlioid algae are observed on the surface near the ascomata, but presumably not lichenized.

DISTRIBUTION. Known only from North America and Iceland.

TYPIFICATION. According to Harris (1973: 23) there is one more specimen of *L. contorta* from Maine part of the same collection, kept at US, which I have not had the opportunity of studying. However, according to Degelius (1942: 30) the type material of *L. contorta* was kept in his own herbarium; this is interpreted as Degelius having designated the holotype. Consequently the second collection from US is regarded as an isotype.

OBSERVATIONS. Harris (1973: 23) suggested that the species may not be distinct from *Leptorhaphis parameca*, usually growing on *Prunus* bark, which is here treated separately (p. 00). However, both taxa differ in ascomatal shape, iodine reaction, and morphology of the ascus apex, and therefore should be maintained as separate species. On the other hand Degelius' collection on *Prunus* bark from North Carolina, as pointed out by Harris, is better referred to *L. parameca*, as the ascomata are surrounded by a basal fringe, and have a bluish iodine reaction in the hymenial gelatin, as well as a truncate ascus apex.

Studies on additional material of *L. contorta* kept at BM showed that Harris' 7474 collection on *Populus* bark from Dickinson County (Michigan), should be referred to *Leptorhaphis lucida*, a species common on *Populus* bark in Europe, with longer and wider ascospores than *L. contorta*, a whitish thallus, and broadly truncate ascus apex. Thus the American material from Ontario, Massachusetts, Michigan, and Wisconsin on *Populus* also mentioned by Harris (1973: 22) may well belong to *L. lucida*.

Leptorhaphis contorta differs from *L. deformis* and *L. laricis*, which also have a truncate to slightly pointed ascus apex, in having larger ascomata and ascospores, and lacking a bluish iodine reaction. *L. epidermidis*, which is common on birch bark, differs in its somewhat shorter and wider ascospores, and the presence of a basal fringe surrounding the ascomata.

ADDITIONAL SPECIMENS. **Iceland**, Austur Skaftaffels sysla, Skaftafell, between the road and the ravine, twig of *Betula*, 10 August 1956, *G. Degelius* (herb. Degelius); loc.cit., Bajarstadaskógur, *Betula* forest rich in herbs, on trunks (also twigs) of *Betula*, 11 August 1956, *G. Degelius* (herb. Degelius). USA [sine loc.], on *Quercus*, 1891, ex Ravenels hb (BM)

4. **Leptorhaphis deformis** Norman in *Bot. Notiser* **1868**: 192 (1868), Type: Finland, Norlandiae, Lyngenfjord, on *Salix*, *J. M. Norman* (O!—holotype).

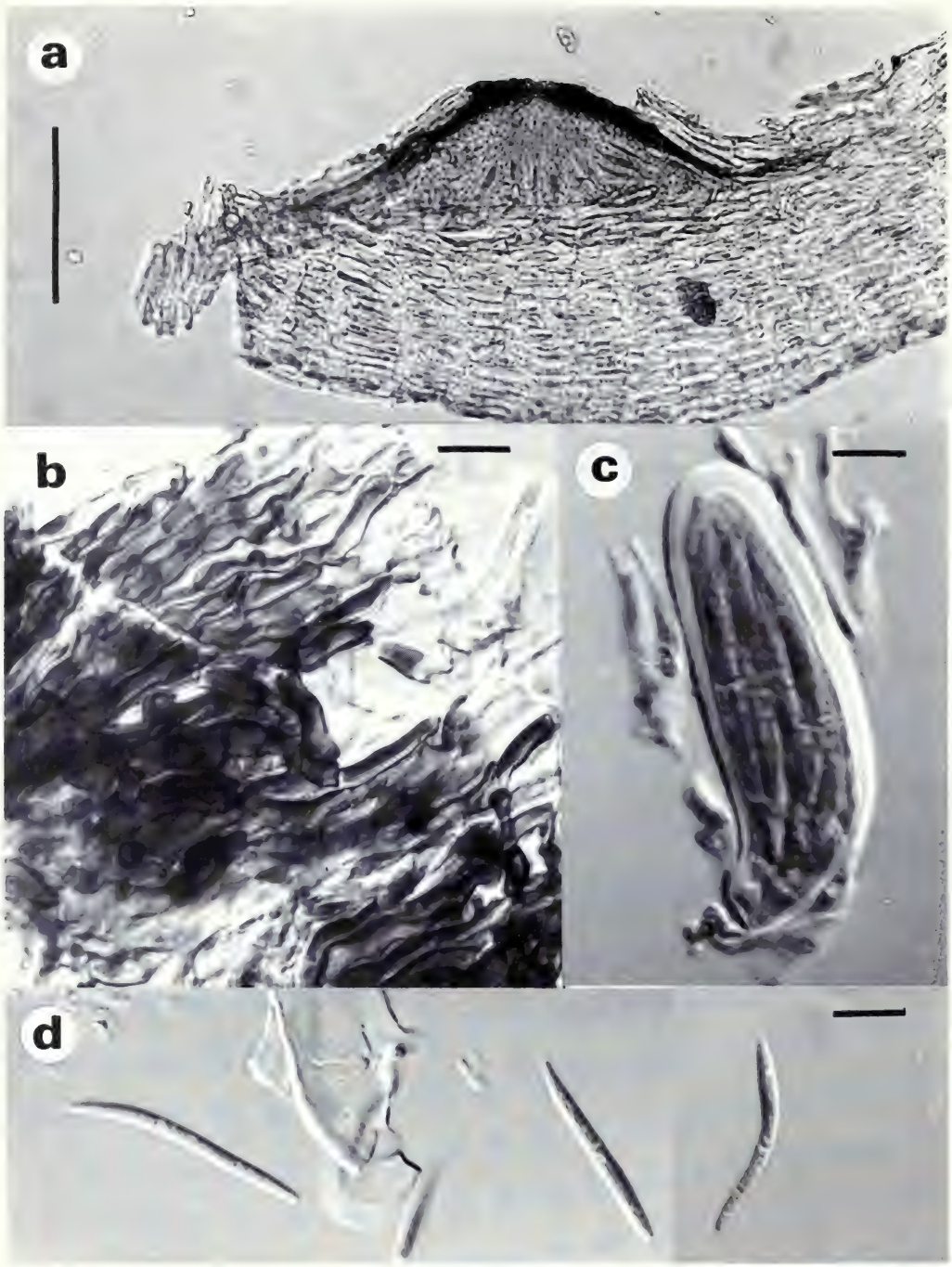


Fig. 5 *Leptorhaphis contorta* Degelius (Degelius–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of involucrellum (surface view): textura epidermoidea-intricata; (c) Ascus and ascospores; (d) Ascospores; scale = 10 μm.

Leptorhaphis confertior Norman in *Ofvers, k. Vetensk, Akad. Förhandl. Stockholm* **41**(8): 40 (1884). Type: Norway, Florö Island, on *Ilex*, *J. M. Norman* (UPS!—holotype).

Fig. 6B, 7.

Thallus: Olivaceous-green to brown, smooth, continuous, not well delimited; superficial to immersed in the substratum, composed of colourless to dark brown, smooth, thin-walled hyphae, *c.* 4 μm wide, cellular and constricted at the septa; associated with trentepohlioid algae, filaments *c.* 8.5–15.5 μm wide.

Ascomata: Blackish, shiny, smooth, scattered singly to confluent, circular, *c.* 140–200 μm diam, not surrounded by a basal fringe; immersed in the substratum, becoming half immersed to superficial, hemispherical, *c.* 85 μm high, dimidiate; ostiole centrally located in small depression. Involucrellum: reddish-brown to black, *c.* 20–30 μm thick, not extending beyond the ascomata; consisting of bark cells

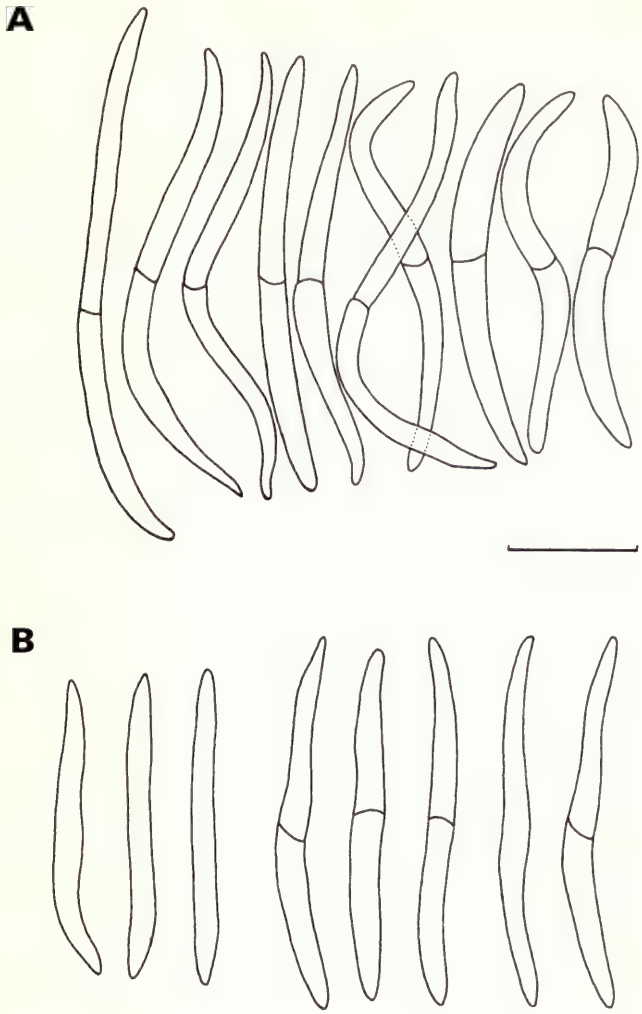


Fig. 6 Ascospore outlines (A) *Leptorhaphis contorta* Degelius (Degelius–holotype); (B) *Leptorhaphis deformis* Norman (O–holotype); scale = 10 μm.

intermixed with reddish to dark brown, nearly black, thin-walled, smooth, isodiametric cells, *c.* 3–4.5 μm diam, forming a clypeus of pseudoparenchymatous tissue of leptodermatous cells. Exciple: intergrading with the involucrellum, colourless to pale brown, *c.* 7.5–12 μm thick; consisting of colourless, smooth, thin-walled, isodiametric cells, forming a textura globulosa-angularis. Hamathecium: of pseudoparaphyses, *c.* 1.5–2 μm wide; bluish-green in iodine. Asci: cylindrical-clavate, short-stalked, 50–60 × 9–14 μm; with two functional layers, the apex of the inner wall truncate to slightly pointed; 8-spored. Ascospores: arranged in one bundle in the ascus, colourless, 0-, 1-septate, fusiform, not observed free, but when in the ascus 15–20 (–25) × 1.5–2 μm, attenuated at the apices.

Conidiomata: Pycnidial, shiny, smooth, circular, scattered individually among the ascomata, *c.* 100–110 μm diam; immersed in the substratum, becoming half-immersed, dimidiate, conical to hemispherical, *c.* 55 μm high; apical ostiole centrally located. Wall: reddish-brown to black, *c.* 12.5–15 μm thick; composed of reddish-brown, thick-walled, smooth hyphae, *c.* 3–5 μm wide, constricted at the septa, intermixed with bark tissue, and not continuing at the base of the conidiomata. *Conidiogenesis*: presumably enteroblastic. *Conidiogenous cells*: somewhat ampulliform, colourless, smooth, thin-walled, *c.* 4 × 3 μm, attached to smaller isodiametric, colourless cells, adjacent to the base and wall of the conidiomata cavity. Macroconidia: colourless, thin-walled, fusiform-filiform, *c.* 20–25 × 1 μm, distal apices sharply ended, aseptate, without appendages or gelatinous sheaths.

ECOLOGY. On bark of *Salix* and *Ilex aquifolium* L., presumably loosely lichenized with trentepohlioid algae.

DISTRIBUTION. Europe, Finland and Norway; known only from these two localities.

TYPIFICATION. Neither *Leptorhaphis deformis* nor *L. confertior* presented typification problems as only single collections from the type locality were located at O and UPS respectively, which should be regarded as the holotype collections.

OBSERVATIONS. Norman (1868, 1884) regarded both *Leptorhaphis deformis* and *L. confertior* as separate species on the basis of the ascomata arrangement and described *L. confertior* for *L. deformis*-like taxa with numerous and confluent ascomata. In other respects, such as ascomatal size, ascus structure and morphology, hymenial gelatin reaction with iodine, and ascospore size, both taxa are rather similar. In my opinion ascomatal arrangement is not sufficient to consider both taxa as separate species, as this could well be affected by environmental factors, e.g. the rate of growth of the substratum.

Keissler (1938) placed *Leptorhaphis deformis* as a synonym of *L. lucida* on the basis of the reportedly similar iodine reaction, and referred *L. confertior* to *'Leptorhaphis' wienkampii* var. *aggregata* [i.e. *Cresporhaphis muelleri* (Duby) Aguirre], although he did not study type material. *L. lucida* and *L. deformis* both have pseudoparenchymatous involucrellum. However, *L. lucida*'s iodine reaction (see p. 112) is negative, while in both *L. deformis* and *L. confertior* the hymenial gelatin turns bluish in iodine. Further, *Cresporhaphis muelleri* belongs to a different genus (see p. 151), erected here on the basis of the distinct ascomatal and ascus structure, and ascospore morphology.

Leptorhaphis deformis differs from *L. laricis*, which also has a bluish iodine reaction and truncate to slightly pointed ascus apex, in having an olivaceous-green thallus and smaller ascospores.

5. **Leptorhaphis epidermidis** (Ach.) Th. Fr. in *Nova Acta Reg. Soc. Scient. Uppsal.* III, **3**: 373 (1860). *Lichen epidermidis* Ach., *Lichenogr. Suec. Prodrom.*: 16 (1798). *Verrucaria epidermidis* (Ach.) Ach., *Method. lich.*: 118 (1803). *Verrucaria epidermidis* var. *vulgaris* Schaerer, *Enum. crit. lich. Eur.*: 220 (1850); nom. illeg. Art. 6.7 (Art. 24.3). *Arthopyrenia epidermidis* (Ach.) Massal., *Rich. auton. lich.*: 167 (1852). *Spermatodium epidermidis* (Ach.) Trevisan, *Consp. verruc.*: 11 (1860). *Campylacia epidermidis* (Ach.) Vainio in *Acta Soc. Fauna Flora fenn.* **49**(2): 187 (1921). Type: Sweden, on *Betula* (BM-ACH 281-282(2)!—lectotype, UPS-ACH 001669(b)!—isolectotype).

Verrucaria oxyspora Nyl. in *Bot. Notiser*: 179 (1851). *Leptorhaphis oxyspora* (Nyl.) Körber, *Syst. lich. Germ.*: 371 (1855). *Pyrenula oxyspora* (Nyl.) Hepp, *Flechten Europas*, no 460 (1857). *Campylacia oxyspora* (Nyl.) Anzi, *Catal. lich. Sondren.*: 12 (1860). *Spermatodium oxysporum*

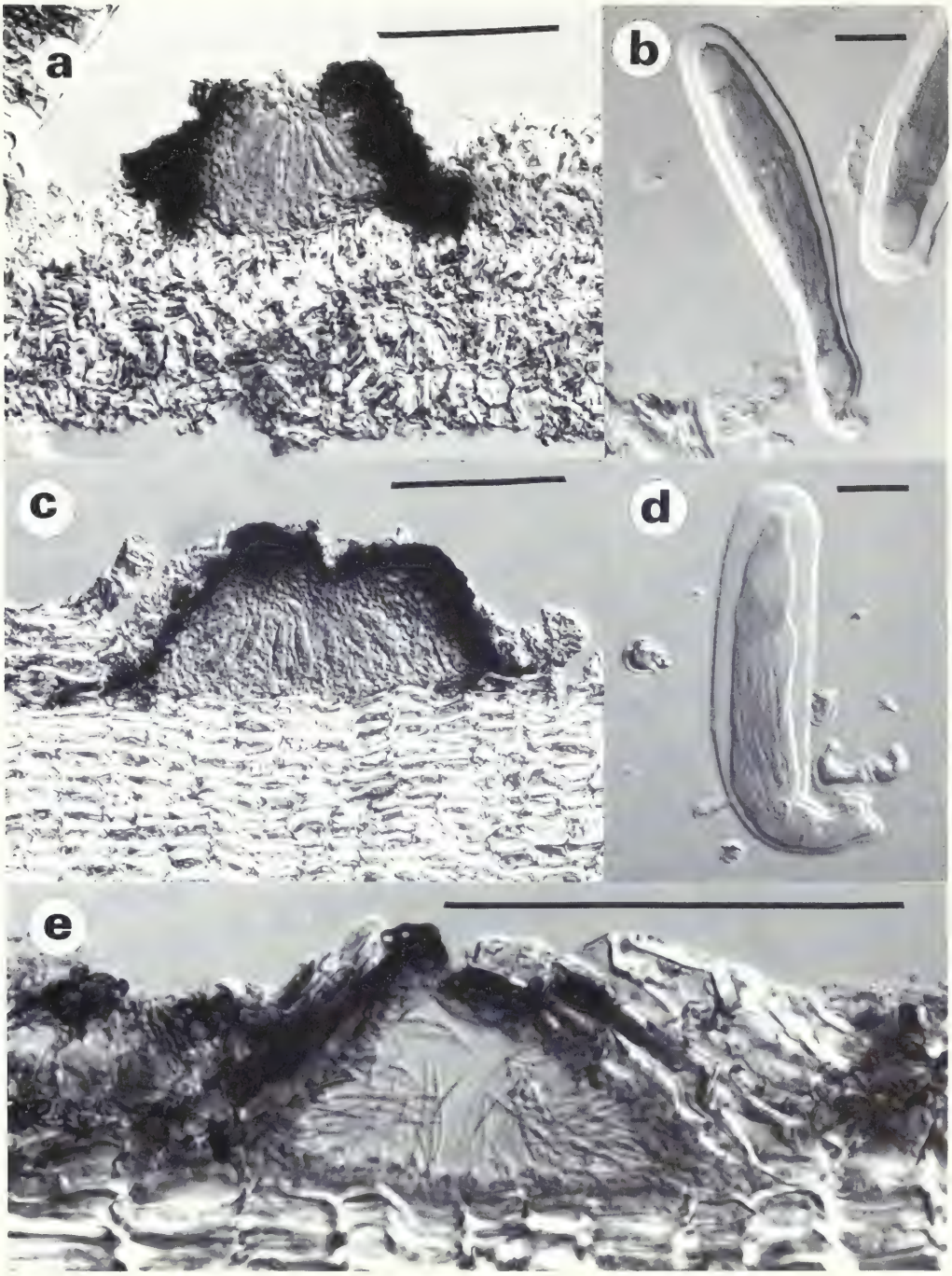


Fig. 7 *Leptorhaphis deformis* Norman (O–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Ascus and immature ascospores; scale = 10 μm; UPS–holotype of *L. confertior*) (c) Vertical section of ascoma; scale = 100 μm; (d) Ascus and immature ascospores; scale = 10 μm; (e) Conidioma and conidia; scale = 100 μm.

(Nyl.) Trevisan, *Consp. verruc.*: 12 (1860). *Arthopyrenia oxyspora* (Nyl.) Mudd, *Man. Brit. lich.*: 306 (1861). *Segestrella oxyspora* (Nyl.) Branth & Rostrup in *Botan. Tidsskr.* **3**: 258 (1869). *Sagedia oxyspora* (Nyl.) Tuck., *Genera lich.*: 266 (1872). *Leptomycorhaphis oxysporae* (Nyl.) Cif. & Tom. in *Atti Ist. bot. Univ. Pavia* V, **10**: 259 (1954). Type: Sweden, Stockholm, 'Danviksbergen, Holmiae', on *Betula*, *W. Nylander* (H-NYL 7503!—holotype, BM!—isotype).

Verrucaria epidermidis var. *albissima* Ach. in *Kungl. Vetensk-Akad. Handl.* **30**: 149 (1809). *Verrucaria albissima* (Ach.) Nyl. in *Notis. Sällsk. Fauna Fl. fenn.* **5**: 282 (1861). *Verrucaria oxyspora* var. *albissima* (Ach.) Roum., *Lich. Gall. exs.* no. 347 (1879); nom. inval. (Art. 33.1). *Arthopyrenia epidermidis* var. *albissima* (Ach.) Boistel, *Nouv. fl. lich.* **2**: 279 (1903). Type: Sweden, on *Betula* (BM-ACH 281–282(3)!—lectotype, selected here; H-ACH 774!—isolectotype, sterile).

Verrucaria epidermidis var. *fusispora* Flotow ex Garov., *Tentam. disp. method. lich. Long.*: 27 (1865). *Campylacia oxyspora* var. *fusispora* (Flotow ex Garov.) Bagl. & Car. in *Atti Soc. crittog. Ital.* **2**(13): 342 (1881). *Verrucaria epidermidis* f. *fusispora* (Flotow ex Garov.) Vainio in *Meddel Soc. Fauna Flora fenn.* **10**: 188 (1883). Type: Italy, Valsesia, 'a Riva e sempre sulla *Betula*' (not located).

Fig. 8, 9.

Thallus: Absent; in fresh material it is possible to observe *Trentepohlia* algae in patches around the ascomata.

Ascomata: Black, matt, smooth, numerous, scattered singly, circular to ellipsoidal, surrounded by a dark fringe, 300–450 μm diam; immersed in the substratum, becoming superficial, hemispherical to applanate, 100–150 μm in height, with a central ostiole, sometimes located in a small papilla. *Involucrellum*: dark brown, *c.* 30 μm thick, extending beyond the ascomata in a basal fringe, *c.* 75 μm in length; composed of bark material intermixed with greenish-black, smooth, thick-walled hyphae, 3–4.5 μm wide, constricted at the septa, forming a textura epidermoidea to intricata, becoming in places a pseudoparenchymatic tissue of mesodermatous cells, covering and surrounding the exciple. Exciple: thin, almost inapparent, composed of colourless to pale brown, smooth and thin-walled hyphae forming a textura porrecta at the base of the ascomata, becoming a pseudoparenchymatous tissue towards the angles of the ascoma cavity. Hamathecium: of pseudoparaphyses, 2–2.5 μm wide; hymenial gelatin not changing colour in iodine, sometimes orange amber. Asci: clavate, short and broad-stalked, 40–65 (–70) × 10–16 μm, usually curved; with two functional wall layers, the outer thin and smooth, the inner thick with a very broad and truncate internal apical beak; 8-spored. Ascospores: arranged in two bundles in the asci, fusiform, arcuate, 24–35 × 2–3.5 μm, 1-septate, attenuated at the apices.

Conidiomata: Pycnidial, smooth, ellipsoidal, matt, scattered singly, *c.* 75 μm diam; immersed in the bark, becoming superficial, globose, with an ostiole centrally located. Wall: continuous, less than 10 μm thick; composed of greenish-black, thick-walled isodiametric cells with enlarged lumen, *c.* 4 μm diam, forming a textura globulosa. Conidiogenous cells: colourless, thin-walled, smooth, more or less lageniform, *c.* 7.5 μm × 1.5–2 μm, arising from colourless, isodiametric cells, adjacent to the conidiomatal wall. Conidiogenesis: probably enteroblastic. Microconidia: colourless, bacilliform, thin-walled, smooth, aseptate, less than 4 μm long. Macroconidia: colourless, fusiform, arcuate, 25 × 1.5–2 μm, aseptate, with few refringent particles.

ECOLOGY. On smooth bark of different *Betula* species, preferentially on young trees, or on bare patches of the trunks and branches; sometimes loosely associated with *Trentepohlia*, but probably not lichenized.

DISTRIBUTION. Widespread, in temperate and cooler regions of the Northern Hemisphere, well-known in North America and Europe.

TYPIFICATION. Vainio (1921: 188) discussed the identity of *Verrucaria epidermidis* (Ach.) Ach. and *Verrucaria epidermidis* β. *albissima* (Ach.) Ach. He recognized the former as a mixed collection of *Arthopyrenia punctiformis* and a species of *Leptorhaphis* Ach.: ' ... specimen dextrum evidenter ad hauc specimen pertinet sed specimen sinistrum forsan ad *Didymellam punctiformem* pertinet ...', although he did not see ascospores; and the latter as an unidentified conidial fungus with acicular-fusiform, curvate conidia, 20–22 × 2–3 μm. Later, Harris (1973: 23) studied some squash mounts from the *Verrucaria epidermidis* sheet in BM [281–282(3)], and also found that labelled 'β. *albissima*' was a pycnidial fungus identical to the taxon in H, and another piece of bark from the same collection, BM-ACH 281–282 (2), was identical with the current concept of *Leptorhaphis epidermidis*. He selected the latter as the lectotype, and considered a second specimen in Hue's herbarium in PC as an isolectotype. Although the study of H-ACH 774, as *Verrucaria epidermidis* var. *albissima* and the lectotype selected by Harris, BM-ACH 281–282 (2), as *Verrucaria epidermidis*, showed that neither of the collections contained ascospores or conidia, the 'squash' mounts studied by Harris were available at BM, and confirmed his observations, so his lectotypification is here fully accepted. I was unable to locate the isolectotype selected by Harris among the original material of the species in Hue's herbarium (PC), but located two packets in the Acharian collection at UPS: *V. epidermidis* (UPS ACH 001669) and *V. epidermidis* var. *albissima* (UPS ACH 001670), both from Sweden. The former contains seven pieces of bark with a mixture of an *Arthopyrenia* species (a), and *Leptorhaphis epidermidis* (Ach) Th. Fr. (b), the latter here accepted as another isolectotype. I was not able to observe any ascospores or conidia in UPS-ACH 001670, although this might be closely related to the *Arthopyrenia* species included in the first packet, since both are externally rather similar and have larger ascomata than *Leptorhaphis epidermidis*.

On the other hand, from the three collections of *Verrucaria epidermidis* var. *albissima* studied, BM-ACH 281–282(3) is here selected as the lectotype, since it is in better condition that the only collection obtained from H-ACH 774, which appears sterile. Here, these are believed to represent the conidial state of *Leptorhaphis epidermidis*. Finally, the collection of *V. epidermidis* var. *albissima* from UPS-ACH 001670, as mentioned above, does not agree with the first two, and is probably better referred to as an *Arthopyrenia* species.

Of the two original collections of *Verrucaria oxyspora* located in H and BM, both in good condition, H-NYL 7503 is considered as the holotype, and that in BM remains as an isotype. Nylander (1851: 179) described *Verrucaria oxyspora* as a fungus with perithecioid dimidiate ascomata, and ascospores becoming attenuated at the apices, differing from Fries, *Lich. Suec. exs.* no. 244 (sub *Verrucaria epidermidis*) in ascospore shape. This exsiccate contains an unidentified *Arthopyrenia* species, referred to by Massalongo (1852: 167, fig. 334) as *Arthopyrenia epidermidis*. However, Nylander (1861: 282) accepted *Verrucaria albissima* (Ach.) Nyl. [i.e. *Verrucaria epidermidis* var. *albissima* Ach.] as the correct name for *Verrucaria oxyspora*. Körber (1855: 371) was also aware of the misapplication of the epithet *epidermidis* to several *Arthopyrenia* species, and so preferred to adopt Nylander's epithet *oxyspora* for *Leptorhaphis epidermidis*. These arguments were not accepted by Th. Fries (1860: 373), whose typification of both the species and the genus has been accepted by later workers, such as Vainio (1921), Clements & Shear (1931), and Harris (1973).

Type material of *Verrucaria epidermidis* var. *fusispora* Flotow ex Garov. was requested from PAV, but was not located (V. Terzo, in litt.). Requests to other herbaria such as WRSL and B were also unsuccessful, consequently the taxon is provisionally included here as a synonym of *Leptorhaphis epidermidis*. However, Garovaglio (1865: 27) described and

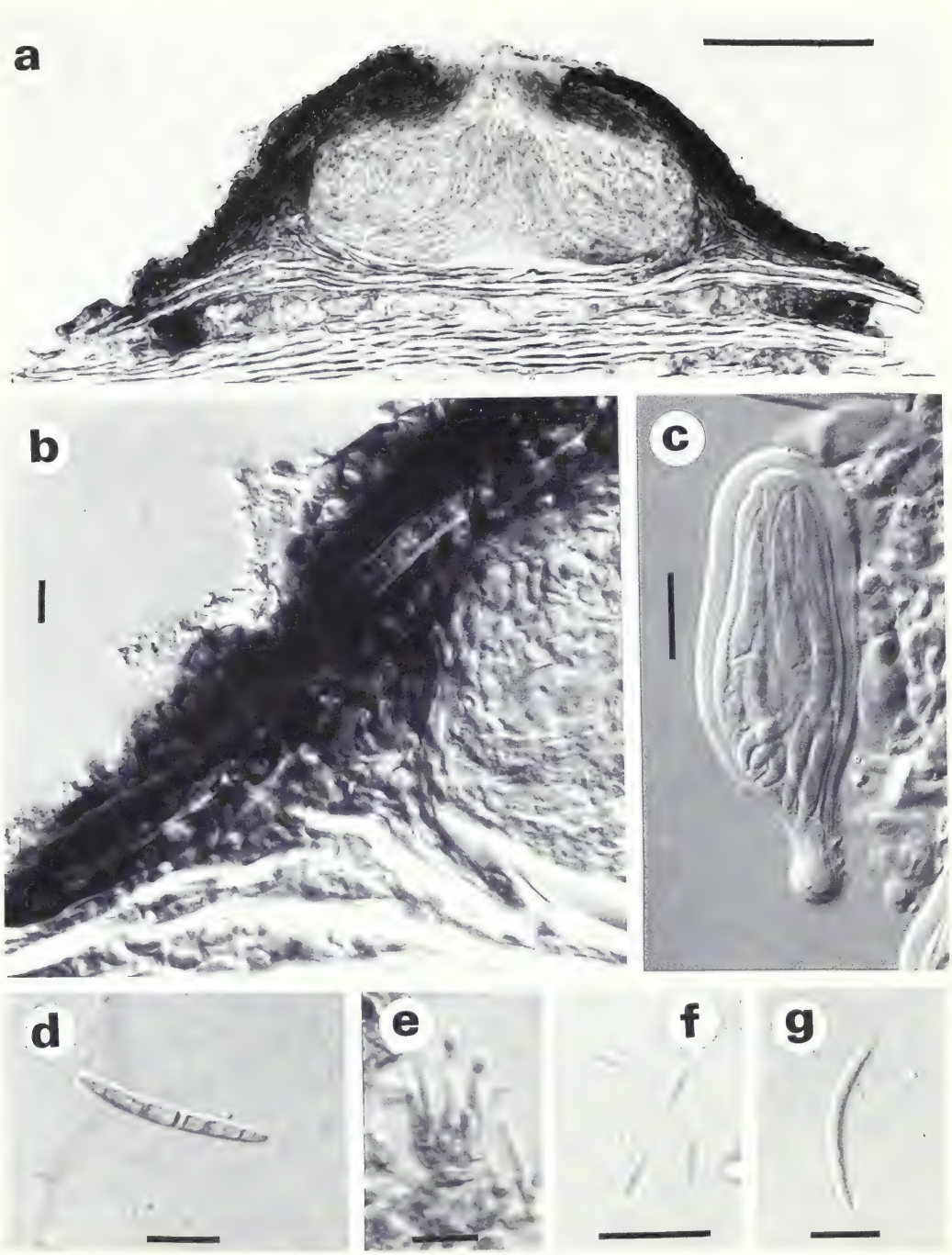


Fig. 8 *Leptorhaphis epidermidis* (Ach.) Th. Fr. (H-NYL 7503–holotype of *Verrucaria oxyspora*) (a) Vertical section of ascoma showing basal fringe; scale = 100 μm; (b) Involucrellum consisting of clypeate tissue; (c) Ascus and ascospores; (d) Ascospore; (e) Conidiogenous cells and microconidia; (f) Microconidia; (g) Macroconidia; scale = 10 μm.

drew a fungus with smaller ascospores (22.8–24.2 × 1.4–2.3 μm), which according to him were always 1-septate, whereas in *V. oxyspora* [i.e. *L. epidermidis*] the ascospores were 1-, 3-septate.

OBSERVATIONS. *Leptorhaphis epidermidis* differs from *L. contorta*, which can also occur on birch bark, particularly in the smaller and wider ascospores, the presence of a characteristic basal fringe surrounding the ascomata, and the broad and truncate ascus apex, instead of the slightly pointed apex of *L. contorta*. *L. epidermidis* and *L. atomaria* have similar ascospore sizes; however, both species clearly differ in the morphology of their ascospores, apically rounded, and on occasions up to 3-septate in *L. atomaria*, while usually 1-septate and apically attenuated in *L. epidermidis*. Both species have a different ascoma morphology in vertical

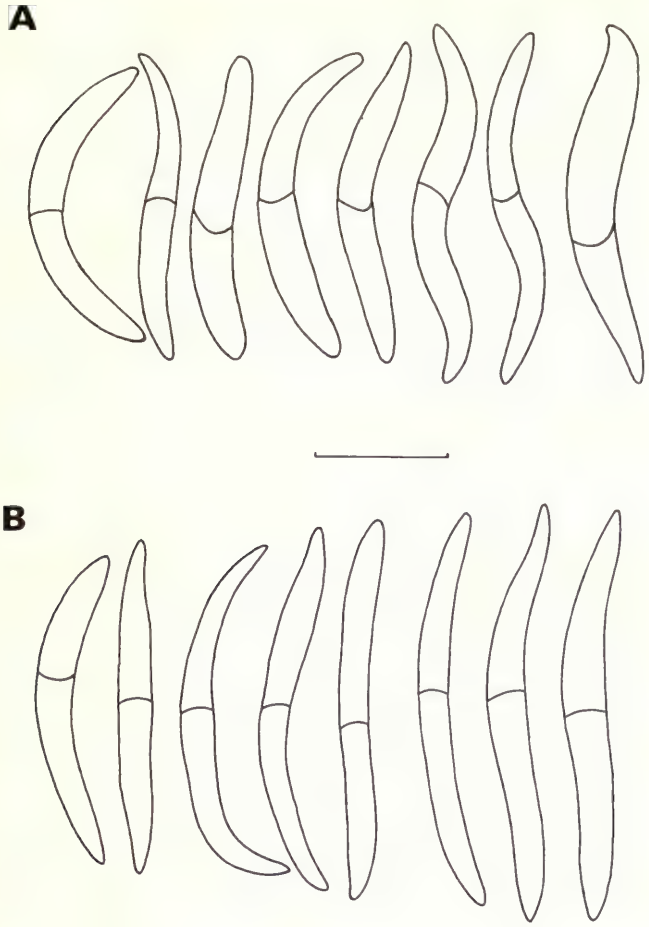


Fig. 9 Ascospore outlines (A) *Leptorhaphis epidermidis* (Ach.) Th. Fr. (UPS–ACH 001669b–isolectotype); (B) H-NYL 7503–holotype of *Verrucaria oxyspora*; scale = 10 μm.

section, *L. epidermidis* being more applanate than *L. atomaria*, and *L. atomaria* lacking a basal fringe to the ascomata.

ADDITIONAL SELECTED SPECIMENS. **Austria**, ... [illegible], Reichenberg, on *Betula*, ... [illegible], 1856, *P.M. Sigmünd* [Holzinger, *Lich. Austriaci exs.*, as *Verrucaria epidermidis* var. *albissima*] (BM). Steiermark, 'Stiria, Ramsanleiten', Schladming, *c.* 800 m, 'ad truncos Betularum', *A. Zahlbruckner* [Zahlbruckner, *Krypt. exs.* no. 1353, as *Leptorhaphis epidermidis*] (BM, B 59669). Vorarlberg, Gr. Vermunt Alpe, oberh. Parthenen, on *Betula*, 10 July 1907, *G. Lettau* (B 33577). **Belgium**, Lomette-Saint-Pierre, 'sur l'écorce du bouleau', *G. Aubert* [Westendorp, *Herb. Crypt. Belg. exs.* no. 1329, as *Verrucaria epidermidis* var. *albissima*] (BM); *loc. cit.*, 'sur l'écorce du Bouleau, souvent mêlé à la variété précédente', *G. Aubert* [Westendorp, *Herb. Crypt. Belg. exs.* no. 1330, as *Verrucaria epidermidis*] (BM). **British Isles**, Eire, Co. Wexford, Oilgate forests, Vassne, *C. Larbalestier* (BM). England, Devon, Dartmoor, Walkham Wood, on *Betula pubescens*, 8 August 1985, *B. Aguirre* (IMI 319627–8). Essex, Brentwood, Thorudon Hall, 1865, *Piggot* (BM). South Hampshire, New Forest, Anses Wood, on *Betula pendula*, 23 June 1968, *B. J. Coppins* 4916 (E); Lindhurst, on *Betula* sp., 29 October 1987, *B. Aguirre* (IMI 319619). Somerset, Sparkford, Hazelgrove School, on *Betula pubescens*, 5 September 1985, *F. Dobson* (IMI 319626). East Sussex, Heathfield (near lakes), on *Betula pendula*, 14 September 1968, *B. J. Coppins* (E). North Yorkshire, Cleveland, Ingleby, Hoggart's Wood, on birches [*Mudd, Lich. Brit. exs.* no. 299, as *Arthopyrenia oxyspora* Nyl.] (BM, E). Scotland, Argyll Main, Glen Euchar, *Betula*, 24 June 1980, *B. J. Coppins* 4916 (E). Berwickshire, 5km SW of Dunns, Langtonlees Cleugh, on *Betula*, 9 October 1981, *B. J. Coppins* 8810 (E). Dumfries, Scarwater, River Nith, on *Betula*, 6 August 1965, *P. W. James* (BM). Dunbarton, Loch Lomond, Torrinch, extreme SW end of island, on *Betula*, 10 October 1979, *B. J. Coppins* 4479 (E). Galloway, Castle Kennedy, on *Betula*, 23 May 1986, *T. S. Caine* (IMI 319625). Grampian, Braemar, Moor of Morrone, beech wood, *J. M. Crombie* (BM). Invernesshire, Glen Nevis, on *Betula*, 21 August 1907, *W. Watson* [*Lichen Exchange Club Br. Isles* no. 1424, as *Verrucaria epidermidis*] (BM). Glen Falloch, *H. B. Holl* (BM). Mid-Perth, near Killin, Finlarig Burn, on *Betula*, September 1960, *U. Duncan* (E). East-Perth, Dunkeld, Loch of Lowes, on *Betula* by lake, 29 August 1977, *B. J. Coppins* 2888 (E). Sutherland, Strathnaver National Nature Reserve, 12 May 1985, *B. Aguirre* (IMI 319630). Wales, Merioneth, Dolgellau, Upper Nant Gwynant, on boles of *Betula*, April 1960, *P. W. James* (BM). **Czechoslovakia**, Bratislava ['Pressburg'], 'ad Betulas', *G. W. Körber* [Körber, *Lich. Sel. Germ. exs.* no. 88, as *Leptorhaphis oxyspora*] (B 59641). Presov ['Eperies'], *F. A. Hazslinsky* (BM, B 59640, 59654). **Finland**, Lapland, 'Lapponia orientalis', on *Betula*, 1863, *N. I. Fellman* [Fellman, *Lichenes arctici exs.* no. 223, as *Verrucaria albissima*] (BM). Ostrobottnia borealis, Simo, Simonkylä, Huttula, Isosuo, on bark of *Betula pubescens*, 8 October 1941, *V. Räsänen* [Räsänen, *Lich. Fenn. exs.* no. 999, as *Campylacia epidermidis*] (BM). Helsinki, on *Betula*, 1858, *W. Nylander* (BM). Tavastia borealis, Laukaa, Normijärvi, Sariniemi, 'ad corticem *Betulae* verrucosae in silva subumbrosa', 16 July 1958, *R. Hakulinen* [Hakulinen, *Lich. Fenn. exs.* no. 1174, as *Campylacia epidermidis*] (BM, B 11421). Tavastia australis, Janakkala, Monikkala, 'ad corticem *Betulae*', 11 August 1917, *R. Elfving* [Räsänen, *Lich. Fenn. exs.* no. 596, as *Campylacia epidermidis*] (BM, B 11424). **France**, 'Hautes de Seine', Ville d'Avrai Wood, on *Betula*, *W. Nylander* [Nylander, *Herb. Lich. Paris exs.* no. 149, as *Verrucaria oxyspora*] (BM). Aisne, St. Simon, bords de Sirroz, 'sur un aulne', 16 June 1894 (PC-HUE 3505/1). Ivelines, Fôret de St. Germain, route verte, 'bouleaux', 18 July 1892 (PC-HUE 3505/1). Brittany, Finistère, Quimperlè, Forêt de Carnoët, on *Betula* sp., 4 September 1986, *B. Aguirre* (IMI 319620). Jura, Dôle, on *Betula*, *J. Müller* (BM). Normandy, 'sur les écorces du bouleau blanc', 1863, *A. F. Malbranche* [Malbranche, *Lich. Norm. exs.* no. 100, as *Verrucaria oxyspora*] (BM, PC). Manche, St. Ebremond, Bois de la Motte, 12 October 1889, 'sur les bouleaux' (PC-HUE 3505/1). Seine et Marne, Fontaine de la Maison-Rouge, on birch, 1892 (PC-HUE 3505/1). Vosgues, Douller, 'corticola', *H. U. V. Claudel* [Claudel & Harmand, *Lich. Gall. exs.* no. 200, as *Verrucaria oxyspora*] (BM, B 59677). **East Germany**, Leipzig, on *Betula*, *R. F. C. v. Uechtritz* (WRSL). Suhl, Thüringer, Arnstadt, Hainwald, 380m, on *Betula*, 19 May 1907, *G. Lettau* (B 59663). Zwickau, near Glasertz, 'an birken', 29 July 1908, *V. Schiffner* (B 59683). **West Germany**, Baden-Württemberg, ... [illegible], on *Betula*, 1890, *H. Rieber* (B 59644, 59629). Heildeberg, Haarlass, 150m, on *Betula*, 21 March 1903, *G. Lettau* (B 33578). Kotingen-Känner, on *Betula*, 14 June 1914, *G. Lettau* (B 59670). Lörrach, Haningen, 330m, on *Betula*, 6 July 1919,

G. Lettau (B 59616). Rheinanen, near Zieken, 'a. älterer *Betula*', 20 August 1916, *G. Lettau* (B 59617). Säckingen, *c.* 400–500m, 'a. *Betula* zimlich im Schotten', 27 June 1915, *G. Lettau* (B 59674). Schwarzwald, Tilisee, near Feldsa, 900m, '*Betula* am Waldrand', 20 July 1948, *O. Behr* (B 59681). Bayern ['Ostpreussen'], Fichtenhain, Grenz, Cranzer Wald, on *Betula*, June 1909, *G. Lettau* (B 59659). Westfalen, Münster, . . . [illegible], Handorf, on *Betula*, September 1862, *T. R. J. Nitschke* (B 59651). **Italy**, Lago Maggiore, Intrasca valley, Trobaso, on *Betula alba*, *F. Baglietto* [Anzi, *Erbar. Crittogam. Ital. exs. b no. 242 (1242). as Campylacia oxyspora*] (BM; B 59725). Baveno, on *Betula*, 1864 (BM). **Norway**, Oppland Province, 'zerstreut an glattrindigen lichtoffenen Mittlestämmen und Unterästen von *Betula pubescens* im *Melanietum olivaceae* (Barkm.) Follman, 600–700m., SW Ph 6.2 lockere Moorbirkengruppen in der Bruchlandschaft unweit Fjellheim', September 1982, *M. Skytte-Christiansen* [Follman, *Lich. exs. sel. Inst. Bot. Univ. Coloniensis* no. 391, as *Leptorhaphis epidermidis*] (BM, O, B 27807). Vestfold, Larvik, 'in cortice betulae', 1840 (O). Nordland, Saltdalen, 'in epidermidis *Betula alba*', April 1820 (O). Fjordane, Hegge paroch., Velfjorden, on birch, *J. M. Norman* (O). Hordaland, Asine, Granvin, *c.* 320m, on *Betula*, *J. J. Havaas* [Havaas, *Lich. Norvegiae exs.* no. 334, as *Leptorhaphis epidermidis*] (O). Akershus, Asker, Grefsenåsen, 16 December 1864, *N. G. Moe* (O). Nllevold, 'in cort. *Betula*', 15 January 1865, *N. G. Moe* (O). Furuval, on birch, 31 January 1891, *F. Kiaer* (O). Troms, Alten, Finmarkice, Garpaholmen, *J. M. Norman* (O). Hadieli Island, Stokmarknes, *J. M. Norman* (O). Aane paroch., Lierne, *J. M. Norman* (O). Gressamo Island, Snaasen, Lidena, J. M. Norman (O). Aust-Agder, Setesdalen-Bykle hd: Bykle nara hotellet, bjørk i asp bestand, c. 635 m, 8 June 1955, *G. Degelius* (O). Tetraak paroch., Brindalen, *J. M. Norman* [sub *L. albissima*] (O). **Poland**, Wroclaw, Obernigk, on *Betula alba*, November 1872, *B. Stein* (WRSL). **Sweden**, . . . [illegible], 'ad corticem Betulae' [Stenhammar, *Lich. Suec. exs.* no. 90, as *Verrucaria epidermidis*] (BM). Närken ['Nerikes'], on *Betula*, *P. J. Hellbom* (BM). Vasterbotten, Umeå, sör fors, slope at Ume River between bridge and electric power dam, on *Betula*, 21 July 1986, *D. L. Hawksworth & O. Eriksson* (IMI 309378). Norrbotten, Lule Lappmark, Porjus paroch., Muddus National Park, on east side of Muddusalvern below footbridge N of Muddusfalet, 66°49′N, 20°10′E, on *Betula*, 23 August 1977, *B. J. Coppins 6127 & L. Tibell* (E). Piteå Lappmark, Arvidsjaür, Råstbergeh, on *Betula*, 1 August 1926, *Henholm* (B 59666). Jåmtland, Storlien, 31 July 1909, *E. P. Vrang* [*Lich. Suecici exs.* no. 2598, as *Leptorhaphis epidermidis*] (B 59642). **Switzerland**, 'an der Rinde junger Birken', *Z. Hepp* [Hepp, *Lich. europ. exs.* no. 460, as *Pyrenula oxyspora*] (E, K, PC HUE 3505/1). Hundschüpf, 'ad truncos *Betulae albae*', 1842 [Schaerer, *Lich. Helv. exs.* no. 107, as *Verrucaria epidermidis* var. *vulgaris*] (BM, PC); loc. cit., [Schaerer, *Lich. Helv. exs.* 108, as *V. epidermidis* var. *albissima* Schaerer, Spicil. p. 56] (E, PC-HUE 3505/1). Vaud, Geneva, *J. Müller* (PC-HUE 3505/1). Altvatergebirges, Oberdorf, near Grüttner, Dürrkunzendorf, near Ziegenbals, on *Betula*, 31 July 1923, *V. J. Grummann* (B 59647). Baselland, Rheinfelden-Olsberg, on *Betula*, 30 November 1913, *G. Lettau* (B 59657). **USA**, Connecticut, Ellsworth, on birch bark, August 1884, *H. A. Green* (BM). Massachussetts, New Bedford Man, on white birch, *H. Willey* (BM). Michigan, Ontonagon County, Porcupine Mountains, Lake of the Clouds, in woods just east of parking lot, 8 September 1965, *R. C. Harris* (BM). Charlevoix County, Beaver Island, Fox Lake, 26 August 1961, *H. A. Imshaug* (BM). Wisconsin, Bayfield, Squaw Point, on Lake Superior at Cornucopia, on *Betula lutea*, 21 August 1965, *I. M. Brodo* (IMI 117362). Wyoming, Blackhills, Crook Co., along North Redwater Creek, 7.3 miles east of Taylor Divide (12 miles N-NE of Sundance), *c.* 1500m, shady north facing birch above stream, 19 August 1960, *C. M. Wetmore* (BM).

6. **Leptorhaphis laricis** (Lahm) Aguirre **comb. nov**.

Leptorhaphis laricis Lahm *in* Arnold, *Lich. exs.* no. 647 (1875); nom. inval. (Art.32.1). *Leptorhaphis tremulae* f. *laricis* Lahm in *Jahresberg. Westfälisch.-Provinz.-Verein.* **13**: 73 (1885). *Leptorhaphis atomaria* f. *laricis* (Lahm) Grumm., *Catalogus Lichenum Germaniae*: 15 (1963). Type: Germany, Westfalen, Büren, Güte Holthausen, on twigs of young larch trees, May 1870, *J. G. F. X. Lahm* (B 37536!—holotype).

Fig. 10, 11A.

Thallus: Inconspicuous.

Ascomata: Black, shiny, smooth, numerous, scattered singly, circular to slightly ellipsoidal, *c.* 150–200 μm, not surrounded by a basal fringe; immersed in the substratum, becoming superficial, hemispherical to applanate, *c.* 70 μm high; ostiole centrally located in a small depression. Involucrellum: dark brown, black in places, *c.* 10–15 μm thick, not extending beyond the ascomata in a basal fringe; consisting of dark brown, smooth, thin-walled hyphae, *c.* 3–4 μm broad, intermixed with bark material, forming a clypeate pseudoparenchymatous tissue of leptodermatous cells. Exciple: colourless to pale brown, intergrading with the involucrellum, thinner, consisting of colourless, thin-walled, isodiametric cells, forming a pseudoparenchymatous tissue of textura angularis. Hamathecium: of pseudoparaphyses, *c.* 1.5–2 μm broad; hymenial gelatin bluish in iodine. Asci: cylindrical-clavate, short-stalked, (35–) 45–55 × 8–17 μm; with two functional layers, the inner wall apex is truncate and slightly pierced by a pore; 8-spored. Ascospores: arranged in one bundle in the asci, slightly twisted, sometimes in two bundles, fusiform, arcuate, 30–40 (–47) × 2–2.5 μm, 1-septate, not constricted at the septum, attenuated at the apices.

Conidiomata: Not observed.

ECOLOGY. On bark of branches of young *Larix* and *Genista germanica* L., presumably saprobic, not causing apparent damage.

DISTRIBUTION. Europe, Germany; known only from Westfalen.

TYPIFICATION. Several collections from the type locality, mainly distributed in Arnold's *Lich. exs.* no. 647, have been studied during the course of this research, but only B 37536 was collected in May 1870 as stated in the protologue; this is therefore accepted as the holotype collection.

OBSERVATIONS. Additional material collected by Beckhaus near Höxter on dry stems of *Genista germanica* was referred by Keissler (1938: 259) to the genus *Ophiobolus* Riess. However, a specimen from the same locality collected by Beckhaus, and located at B, is here accepted as *Leptorhaphis laricis* after close examination.

The external appearance and size of *Leptorhaphis laricis* ascomata recalls those of *L. tremulae* (p.00), but the species

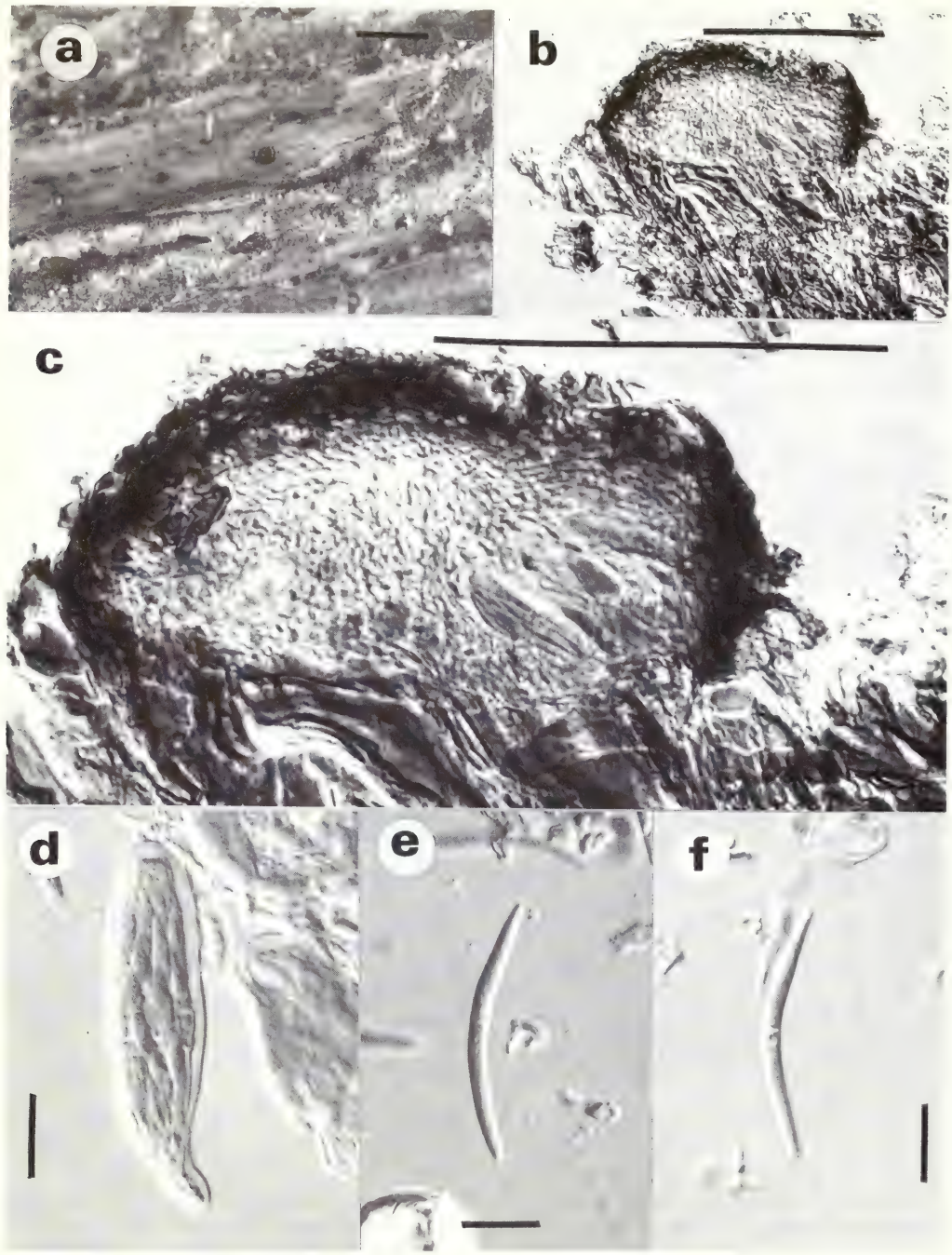


Fig. 10 *Leptorhaphis laricis* (Lahm) Aguirre (B 37536–holotype) (a) Surface view; scale = 500 μm; (b), (c) Vertical sections of ascomata; scale = 100 μm; (d) Ascus and ascospores; (e), (f) Ascospores; scale = 10 μm.

differs in its longer and narrower ascospores, as well as in having 8-spored instead of polysporous asci. *L. laricis* also resembles *L. parameca* (p. 00) in the reaction with iodine and ascospore morphology and size, but the ascomata of *L. parameca* are larger and ellipsoidal, surrounded by a basal fringe, and the ascus apex is always truncate. *L. contorta*, also with a somewhat similar ascospore morphology and size, differs in the iodine reaction, ascus apex, and larger ascomata size.

ADDITIONAL SPECIMENS. **Germany**, Westfalen, Büren, Güte Holthausen, on twigs of young *Larix* trees, July 1875, *J. G. F. X. Lahm* [Arnold, *Lichen. exs.* no. 647, as *Leptorhaphis laricis* Lahm] (B 59620, BM, PC-HUE 3505/4). Höxter, on *Genista germanica*, 1878, *K. Beckhaus* (B 37549).

7. **Leptorhaphis lucida** Körber, *Parerg. lich.*: 384 (1865). *Arthopyrenia lucida* (Körber) Müll. Arg. in *Flora, Jena* **66**:

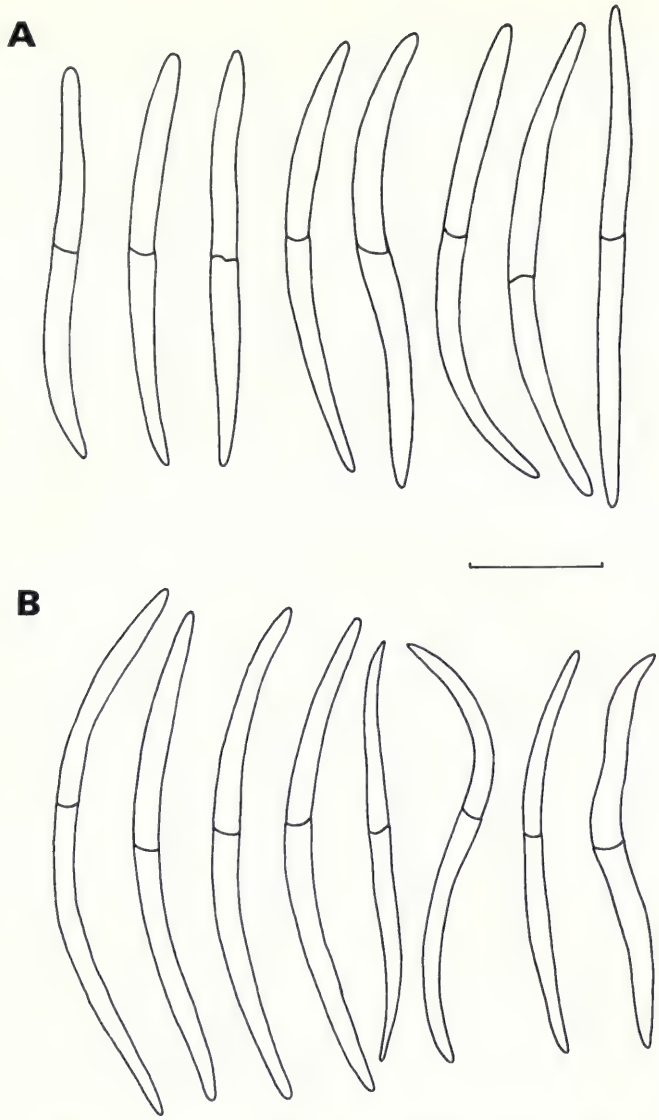


Fig. 11 Ascospore outlines (A) *Leptorhaphis laricis* (Lahm) Aguirre (PC–HUE 3505/4); (B) *Leptorhaphis maggiana* (Massal.) Körber (BM–lectotype); scale = 10 μm.

319 (1883). *Leptorhaphis tremulae* var. *lucida* (Körber) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1(2): 256 (1938). Type: Czekoslovakia, Presov ['Eperies'], near Radais, on *Populus, Cl. Hazslinsky* (L!—holotype).

Campylacia psilotera var. *vermifera* Räsänen in *Suomal. elain-ja kasvit. Seur. van kasvit. Julk.* **20**(3): 34 (1944). Type: USSR, Leningrad Region ['Fennia: Ik, Sakkula, Kovero-oja], 'Ad corticem laevigatum *Populi tremulae*', 15 August 1917, *V. Räsänen* (H!—holotype).

Fig. 12, 13.

Thallus: Whitish-grey, smooth, continuous, not well delimited; superficial to immersed, consisting of colourless to pale brown, smooth, thin-walled hyphae, *c.* 2–3 μm wide, constricted at the septa; associated with trentepohlioid algae.

Ascomata: Black, shiny, circular, not surrounded by a basal fringe, scattered singly, *c.* 300–500 μm diam; at first immersed in the substratum, but soon becoming superficial, hemispherical, *c.* 90–180 μm high; ostiole centrally located in a small depression. Involucrellum: dark brown almost black, *c.* 25–35 μm thick, not extending beyond the ascomata in a basal fringe; consisting of dark brown, thin-walled, smooth hyphae, about 3.5–4 μm thick, intermixed with host tissue, forming a pseudoparenchymatous tissue of leptodermatous and isodiametric cells of textura angularis in squash mounts, becoming in places a textura intricata. Exciple: colourless to pale brown, intergrading with the involucrellum and slightly thinner, also forming a pseudoparenchymatous tissue of leptodermatous cells, recalling a textura angularis. Hamathecium: of pseudoparaphyses, *c.* 2–2.5 μm wide; hymenial gelatin not changing in iodine. Asci: cylindrical-clavate, short and broad-stalked, *c.* 60–73.5 × 10.5–14.75 μm, with two functional layers, the outer thin and smooth, the inner becoming thicker at the apex, which is broad and truncate; 8-spored. Ascospores: arranged in two bundles in the asci, fusiform, slightly curved, *c.* 45–65 (–70) × 2.5–4 μm, 1-septate, attenuated at the apices.

Conidiomata: Not observed.

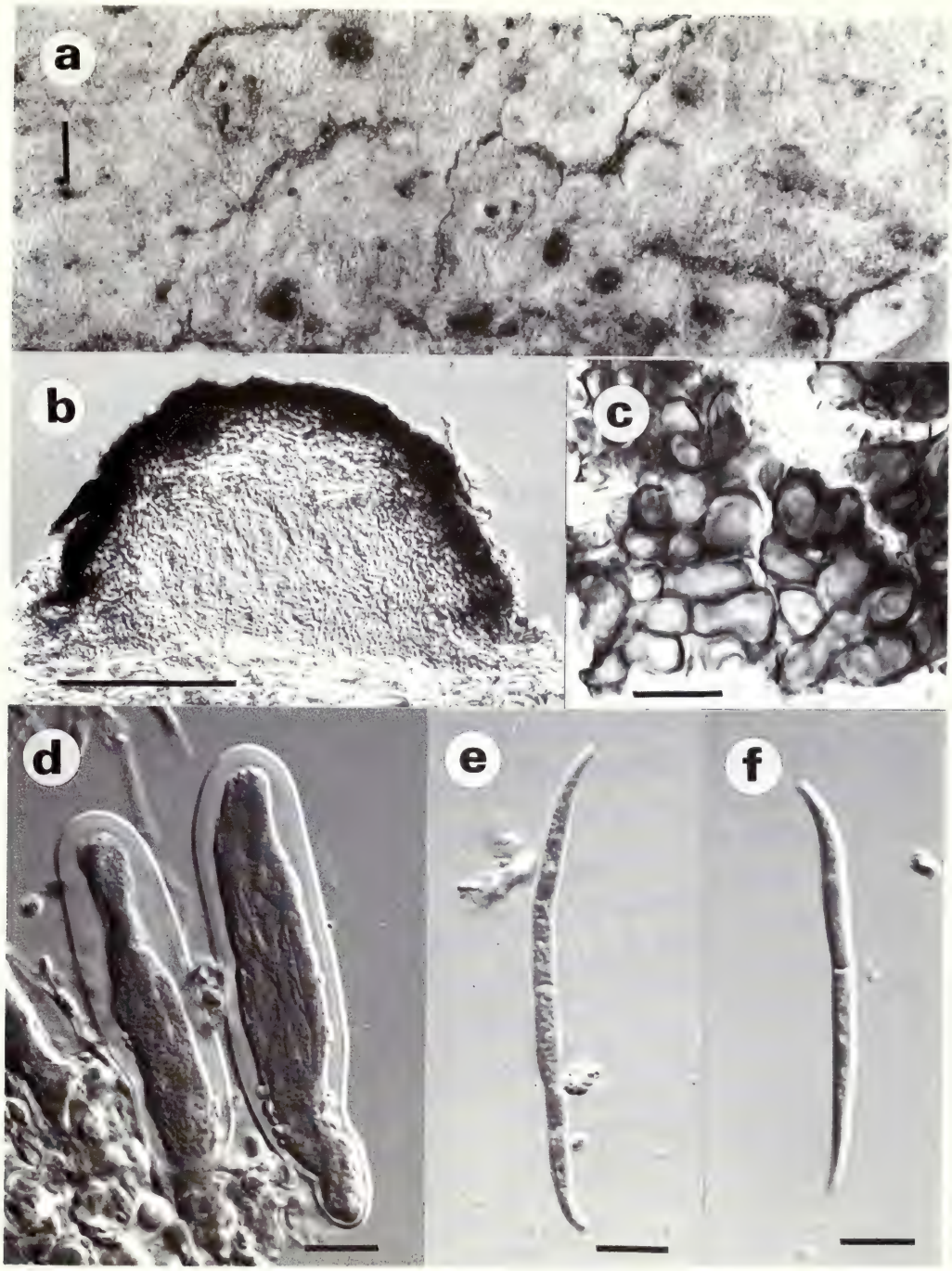


Fig. 12 *Leptorhaphis lucida* Körber (L–Körber *Lich. Sel. Germ. exs.* no. 262) (a) Surface view; scale = 500 µm; (b) Vertical section of ascoma; scale = 100 µm; (c) Detail of involucrellum (surface view): textura globulosa; (d) Asci; (e), (f) Ascospores; scale = 10 µm.

ECOLOGY. On bark of different species of *Populus*, forming white patches; presumably lichenized with trentepohlioid algae.

DISTRIBUTION. Collected from central and northern Europe in the middle of the last century, but I am not aware of any recent collections, except for North America (Michigan, Dickinson Country) where Harris (1973) collected it as *Leptorhaphis contorta*. Presumably all the records of *L. contorta* on *Populus* bark mentioned in his article may be better referred to *L. lucida*. Probably widespread in the northern hemisphere, but overlooked.

TYPIFICATION. A specimen from Körber's Typenherbar in L collected on *Populus* bark from the locality mentioned in the description is here regarded as the holotype. Material distributed in exsiccate by Körber from the same locality are here included as syntypes.

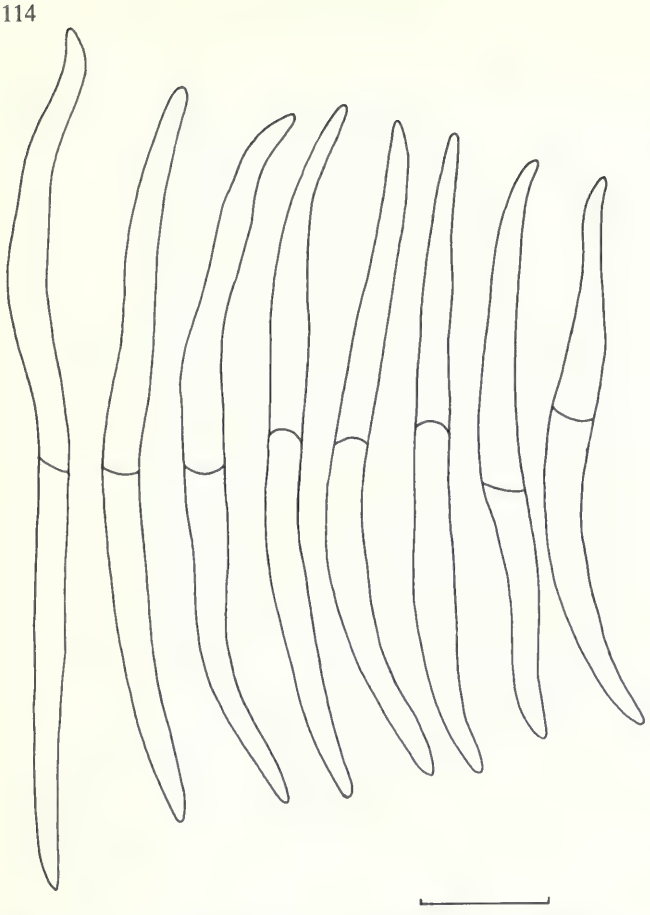


Fig. 13 Ascospore outlines of *Leptorhaphis lucida* Körber (L–holotype); scale = 10 μm.

On the other hand, the single collection of *Campylacia psilotera* var. *vermifera* studied from H is here regarded as the holotype since aggrees with the protologue.

OBSERVATIONS. There are two other species also occurring on *Populus* bark: *Leptorhaphis atomaria* and *L. tremulae*. Keissler (1938) referred *L. lucida* as a variety of *L. tremulae* while *L. atomaria* was included as a synonym of an *Arthopyrenia* following Zahlbruckner's *Catalogus lichenum universalis* (1922). Recently Hawksworth et al. (1980) accepted *L. atomaria* and *L. tremulae* as synonymous since both epithets were traditionally used and confused for numerous specimens here referred to as *L. atomaria*, usually on trunks of *Populus* species, with the hymenial gelatin always bluish in iodine, and 6-, 8-spored asci. Instead, *L. tremulae*, less common than *L. atomaria*, is usually present on twigs and branches of *Populus*, the ascomata is somewhat smaller and surrounded by a basal fringe, the hymenial gelatin does not change colour in iodine, asci are 8-, 16-spored, and the ascospores smaller. Like *L. tremulae*, *L. lucida* lacks an iodine reaction in the hymenium, but differs in the morphology of the ascomata, lack of a basal fringe, and in having 8-spored asci. The ascospores are much longer in *L. lucida* than in the other two species and in the ascomatal tissue type and 8-spored asci resembles *L. atomaria*. The combination of characters are sufficient to consider these three taxa as different species.

ADDITIONAL SPECIMENS. **Austria**, Oberösterreich, near Nuremsmünster, ... [illegible], on *Populus* bark, 25 November 1861, *I.S. Poetsch* (B 59622). **Czekoslovakia**, Presov ['Eperies'], near Radais, on trunks of *Populus tremula*, 1862, *Cl. Hazslinsky* [Körber, *Lich. Sel. Germ. exs.* no 262, as *Leptorhaphis lucida*] (L—syntype; BM—2 syntypes); loc. cit., on *Populus nigra*, *Cl. Hazslinsky* (BM); loc. cit., *Cl. Hazslinsky* (WRSL, L, B 59627). **West Germany**, Bayern ['Ostpreussen'], Galtgarben, on *Populus tremula*, 23 August 1902, *G. Lettau* (B 59706). **Switzerland**, on bark of *Populus tremula*, 1857, *P. Hepp* [Hepp, *Flech. Eur. exs.* no. 478, as *Thrombium sticticum* var. *minutissimum*] (K). **USA**, Michigan, Dickinson Co., Spruce-Jack pine-poplar woods along road into O'Neil Lake, Campground, on *Populus*, 14 August 1971, *R. C. Harris* (BM). [Sine loc.], on *Populus*, 1891, *H. W. Ravenel* (BM).

8. **Leptorhaphis maggiana** (Massal.) Körber, *Parerg. lich.*: 386 (1865). *Campylacia maggiana* Massal., *Sched. Crit.*: 74 (1856). *Spermatodium maggianum* (Massal.) Trevisan, *Conspect. verruc.*: 12 (1860). *Verrucaria maggiana* (Massal.) Stizenb. in *Jährb. St. Gall. Naturw. Ges.* **22**: 513 (1882). *Leptorhaphiomyces maggianae* (Massal.) Cif. & Tom. in *Atti Ist. bot. Univ. Lab. Crittog. Pavia* V, **10**: 58 (1953). Type: Italy, Verona Province, Villa di Palazzuolo, on *Corylus avellana*, *P. Maggi* [Massalongo, *Lich. exs.* no. 109, as *Campylacia maggiana*] (BM!—lectotype, selected here,—isolectotype [sterile]; PAD!—isolectotype).

Fig. 11B, 14.

Thallus: Inconspicuous; trentepohlioid algal cells occasionally seen on the surface.

Ascomata: Dark-brown to black, shiny, smooth, numerous, scattered singly, circular, only slightly ellipsoidal, *c.* 135–300 μm diam; at first immersed in the substratum, later becoming superficial, hemispherical to applanate, sometimes mammiform, 40–70 μm high; ostiole centrally located in a small papilla. Involucrellum: dark brown to greenish-black, *c.* 15 μm thick, covering the exciple, sometimes extending in a basal fringe, *c.* 35–55 μm long; composed of bark material intermixed with reddish-brown to greenish-black, smooth, thin-walled hyphae, *c.* 3.5–5.5 μm broad, slightly constricted at the septa, forming a clypeate tissue of textura epidermoidea to intricata. Exciple: colourless to greenish-black, *c.* 15 μm thick, slightly thicker at the angles of the ascomatal cavity, intergrading with the involucrellum; consisting of colourless to greenish-black, thin-walled, isodiametric cells, with an enlarged lumen, forming a textura angularis. Hamathecium: of pseudoparaphyses, *c.* 2–2.5 μm wide; hymenial gelatin yellowish in iodine. Asci: cylindrical-clavate, short-stalked, *c.* 50–55 × 9–11 μm; with two functional layers, the outer thin and smooth, the inner thicker, expecially at the apex, which is broad and truncate; 8- spored. Ascospores: arranged in a fascicle, helically twisted, filiform, arcuate to sigmoid, slender, (25–) 30–45 × 1.5–2.5 μm, 1–, occasionally 3-septate, attenuated at the apices.

Conidiomata: Pycnidial, black, shiny, circular to ellipsoidal, scattered singly among the ascomata, 100–150 μm diam; immersed in the substratum, becoming superficial and somewhat flat at the base; opening by a central ostiole. Wall: dark brown to greenish-black *c.* 7–10 μm thick; consisting of dark-brown, thin-walled, isodiametric cells, intermixed with bark material forming a clypeus of textura angularis. Conidiogenous cells: colourless, smooth, thin-walled, ampulliform-lageniform, *c.* 5–10 × 1.5–2.5 μm, occasionally branching, arising from colourless, smooth, thin-walled, isodiametric

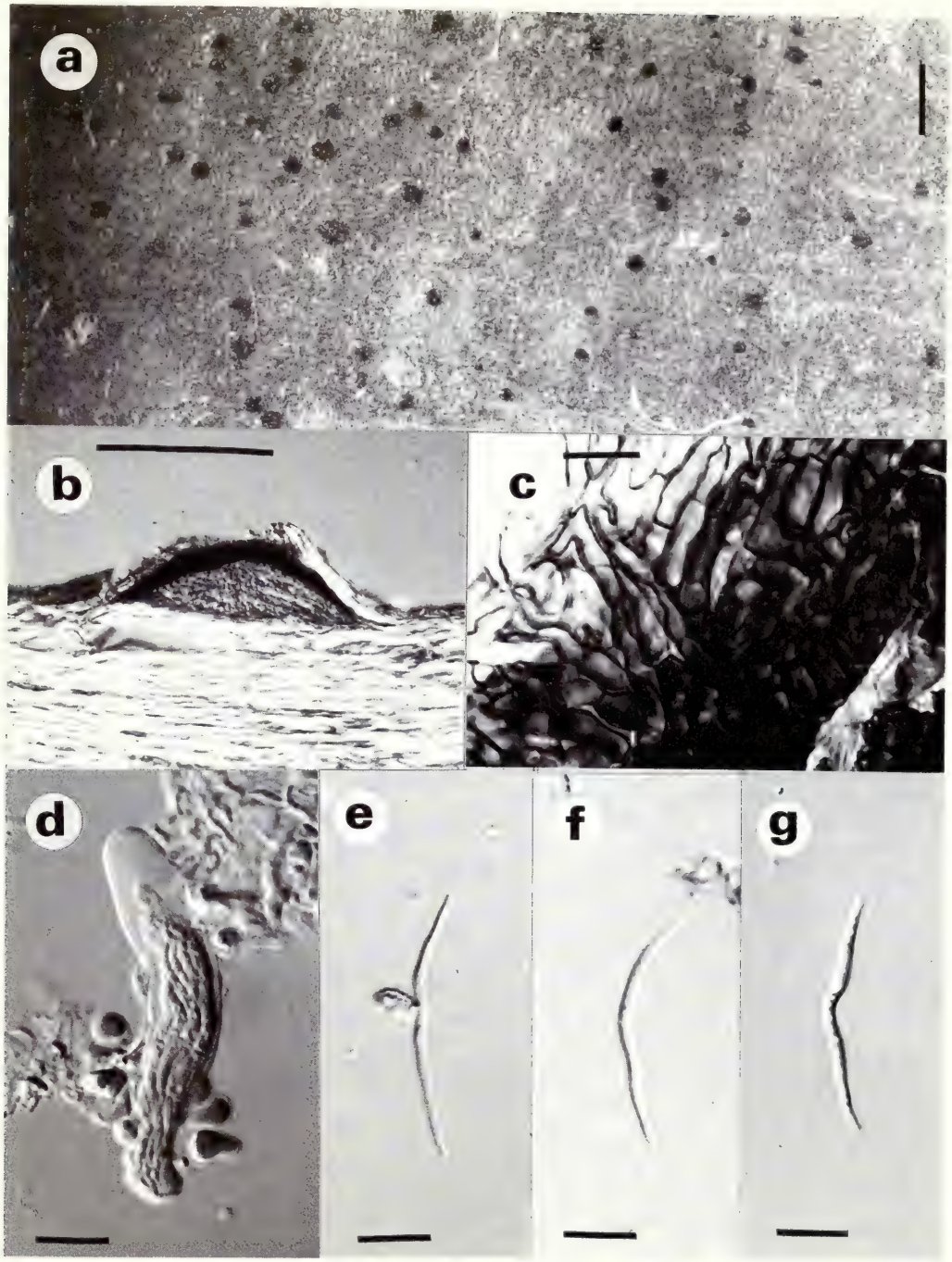


Fig. 14 *Leptorhaphis maggiana* (Massal.) Körber (BM–lectotype) (a) Surface view; scale = 500 μm; (b) Vertical section of ascoma; scale = 100 μm; (c) Detail of involucrellum (surface view): textura epidermoidea-intricata; (d) Ascus and ascospores; (e), (f), (g) Ascospores; scale = 10 μm.

cells adjacent to the pycnidial wall. Conidiogenesis: presumably enteroblastic. Microconidia: colourless, smooth, thin-walled, bacilliform, *c.* 3.75 × 1–1.5 μm. Macroconidia: colourless, smooth, thin-walled, filiform, arcuate, *c.* 20–25 × 1–1.5 μm, 1-septate, not constricted at the septa.

ECOLOGY. On bare and smooth bark of *Corylus avellana* L. and young *Quercus robur* L., presumably saprobic, not causing any apparent damage; trentepohlioid algal cells seen on the surface, but not lichenized.

DISTRIBUTION. Europe, known from Austria, Italy, Germany and Switzerland in the second half of the last century; it has recently been collected in two localities of the British Isles: South Devon (D. L. Hawksworth and B. Aguirre) and Scotland (B. J. Coppins). Apparently rare.

TYPIFICATION. Material was requested from VER but not located. Instead, three packets of Massalongo's type collection *Lich. exs.* no. 109 were obtained from BM and PAD. One of the specimens from BM is sterile, and from the remaining two, the material from BM is here selected as a lectotype since it is in particularly good condition, and ascomata are more abundant on it than the specimen kept at PAD.

OBSERVATIONS. The species has been on occasion mistaken for *Leptorhaphis quercus* (Beltram.) Körber [= *Campylacia quercus* Beltram (p. 178)], as in Körber's (1868) *Lich. Sel. Germ. exs.* no. 324 and the material from Insbruck (PAD 2890). It is possible that both species are closely related, albeit Beltramini (1858) described the latter as having minute ascomata, smaller than *L. maggiana*. I was unable to locate type material of *L. quercus* so the identity of the taxon still remains uncertain (p. 178).

Leptorhaphis maggiana differs from the rest of the species accepted in the genus in having long but narrow ascospores, differing from *L. psilotera*, also with long and narrow ascospores, in the iodine reaction, which is always bluish in the latter, and the presence of conidiomata. One other species is found on *Quercus* bark: *Leptorhaphis contorta*. *L. maggiana* differs from that species in the smaller ascomata, the reddish-brown hyphae in the involucrellum, the ascus apex which is always truncate, and the presence of 1-, 3-septate ascospores.

ADDITIONAL SPECIMENS. **Austria**, Innsbruck, Hungerburg, on *Corylus*, 1907 (PAD 2890). **British Isles**, Scotland, Argyll Main, Loch Creran, Glasdrum National Nature Reserve, on *Corylus* in south facing ashwood, 27 September 1985, *B. J. Coppins* et al. (E). England, South Devon, Slapton Ley Nature Reserve Wood, on *Corylus avellana*, 4 August 1985, *D. L. Hawksworth & B. Aguirre* (IMI 319618). **West Germany**, Baden-Württemberg, H ... [illegible], gegen Wolfartweiben (b. Woldice), on *Corylus* or *Quercus*, May 1885, Herten (B 59702). **Switzerland**, Geneva, Salève, *J. Müller* (B 59703). Geneva, Salève Mountain, 'supra pagum Dossey', on young *Quercus*, *C. A. F. W. Müller* [Körber *Lich. Sel. Germ. exs.* no. 324 as *Leptorhaphis quercus*] (B 59601).

9. **Leptorhaphis oleae** (Massal.) Körber, *Parerg. Lich.*: 386 (1865). *Sagedia oleae* Massal., *Symm. lich.*: 96 (1855). *Limboria oleae* (Massal.) Trevisan, *Consp. verruc.*: 15 (1860). Type: Italy, Verona Province, Grezzana, Carara, on young trunks of *Olea europea*, 1854, *A. B. Massalongo* (VER!—holotype).

?*Leptorhaphis epidermidis* var. *olivetorum* G. Samp. in *Bolm Soc. Broteriana* II, **2**: 4 (1923). Type: Portugal, Penedo de Saüdade, 'cascas das oliveiras', January 1922, *G. Sampaio* (not located).

Fig. 15, 16A.

Thallus: Inconspicuous.

Ascomata: Black, shiny, smooth, numerous, scattered singly, somewhat circular, *c.* 200–300 μm diam; immersed in the substratum, soon becoming half superficial, applanate, mammiform, dimidiate, *c.* 55–75 μm high. Involucrellum: dark brown to greenish-black, *c.* 15–20 μm thick, not extending beyond the ascomata in a basal fringe; consisting of bark cells intermixed with brown to greenish-black, smooth, thick-walled hyphae, *c.* 4 μm broad, constricted at the septa, forming a clypeus of elongated radiating cells of textura intricata, becoming in places a pseudoparenchymatous tissue of leptodermatous cells. Exciple: not differentiated from involucrellum. Hamathecium: of pseudoparaphyses, *c.* 1.5–2 μm broad; hymenial gelatin not changing colour in iodine. Asci: cylindrical-clavate, short and broad-stalked, 52.5–58.5 × 14.5–20.5 μm; with two functional wall layers, the outer thin and smooth, the inner thicker, specially at the apex, which is broad and truncate, sometimes slightly indented; 8-spored. Ascospores: arranged in one or two bundles in the asci, fusiform, sometimes sigmoid, 30–40 × 3–4.5 μm, 3-, 5-septate, apices attenuated.

Conidiomata: Not observed.

ECOLOGY. On bark of *Olea europaea* L., 'Lauriers roses' (?*Nerium oleander* L.), and *Rhamnus lycioides* L., generally on young trunks, not causing any apparent damage; presumably saprobic.

DISTRIBUTION. Europe and North Africa. Presumably widespread in the Mediterranean region, with somewhat similar distribution as its substratum: olive trees. Kusan (1953: 89) reported the species from a few localities in Dalmacia (Yugoslavia), growing also on *Olea* and *Nerium oleander*.

TYPIFICATION. Type material containing numerous pieces of bark was located in Massalongo's herbarium at VER. This single collection can therefore be considered as the holotype (Art.9.1).

OBSERVATIONS. This species differs from the other taxa included within *Leptorhaphis* in having 3-, 5-septate ascospores always. Only *L. psilotera* presents mostly 3-septate ascospores, but those differ from 3-septate ascospores of *L. oleae* in their bigger length: breadth ratio, and both species can also be separated on their iodine reaction.

Two other taxa have been described from olive trees: *Leptorhaphis michaudi* B. de Lesd. (p. 177) and *Leptorhaphis epidermidis* var. *olivetorum* G. Samp. (p. 178). Type material of the former was probably destroyed with Bouly de Lesdain's herbarium in 1940 (Laundon, 1979), while I was unable to obtain type material of the latter requested from Sampaio's herbarium in Porto (R. Salema in litt.). Nevertheless, according to its description, *L. michaudii* does not seem to be closely related to *L. oleae*, since it has entire perithecia instead of dimidiate and sometimes semicircular ascospores. On the other hand, *L. epidermidis* var. *olivetorum* is described as having a thin thallus, dimidiate perithecium, cylindrical asci, very thick at the top, and acicular-subcylindrical ascospores, 1-, 7-septate (15–37 × 2.5 μm), and may well be synonymous with *L. oleae*.

Two collections of C. Flagey *Lich. Alger. exs.* no. 376 (sub *Leptorhaphis oxyspora* (Nyl.) Körber [i.e. *Leptorhaphis epidermidis* (Ach.) Th. Fr.]) have been studied in PC-HUE. This exsiccate is a mixed collection where one of the packets contained a species of *Arthopyrenia*, presumably *A. punctiformis* s. lat., and the second is not *L. epidermidis* but a typical specimen of *L. oleae*.

ADDITIONAL SPECIMENS. **Algeria**, Teksenna, on 'Lauriers roses' [Flagey, *Lich. Alger. exs.* no. 376, as *Leptorhaphis oxyspora*] (PC-HUE 3505/1). **Italy**, Verona Province, Grezzana, Carara, on young trunks of *Olea europea*, *A. B. Massalongo* [Anzi, *Lich. rar. Veneti exs.* no. 138, as *Sagedia oleae*] (BM). **Spain**, Cataluña, Tarragona, Punta de la Mora, 20 m, CF55, on *Rhamnus lycioides*, 10 February 1987,

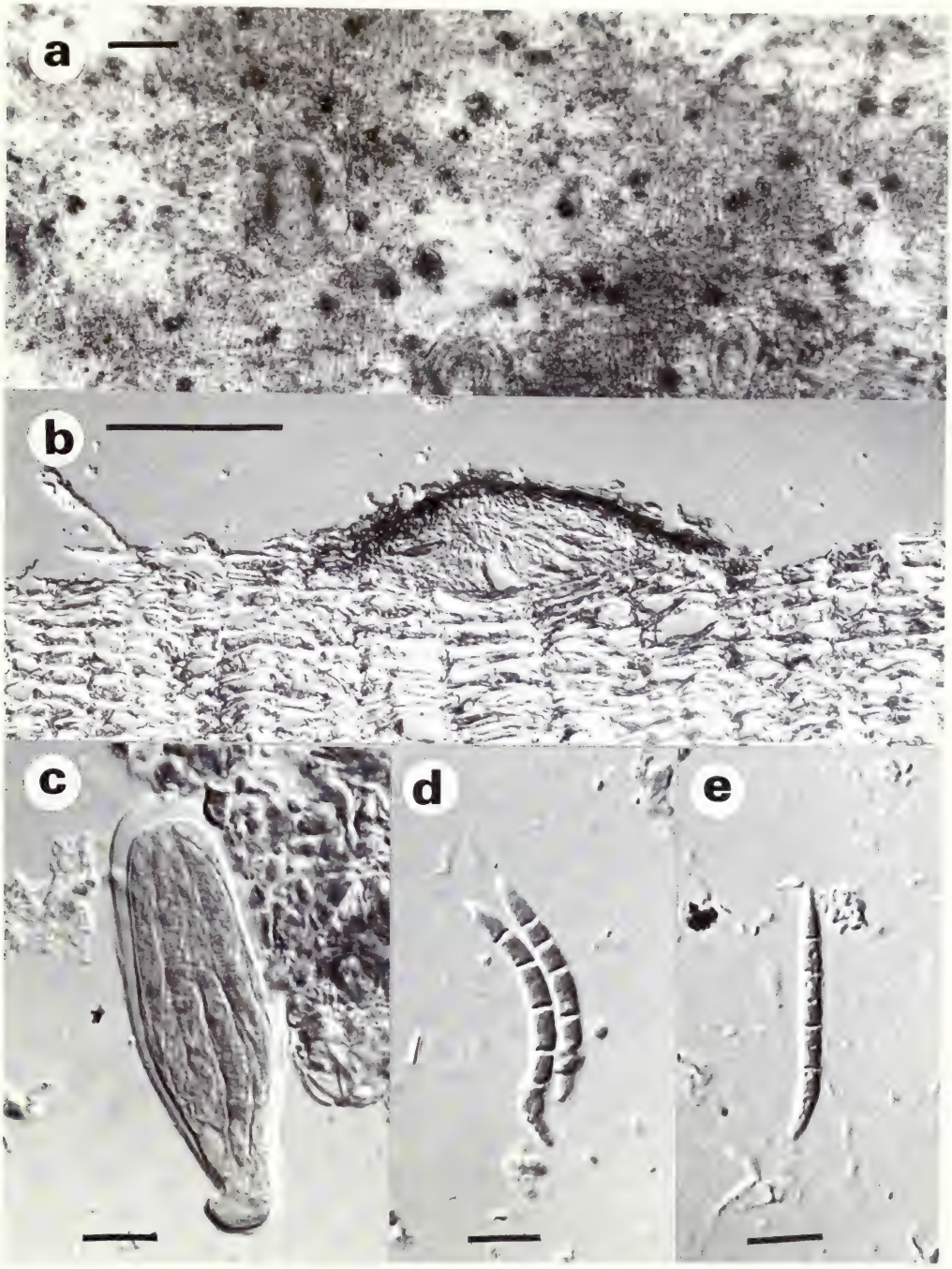


Fig. 15 *Leptorhaphis oleae* (Massal.) Körber (VER–holotype) (a) Surface view; scale = 500 μm; (b) Vertical section of ascoma; scale = 100 μm; (c) Ascus showing ascospores arranged in two bundles; (d), (e) Ascospores; scale = 10 μm.

M. Giralt (BCC 3744). Valencia, rin Xiiqué, entre Xalans i Cofrents, 400 m, on *Nerium oleander*, 8 April 1988, *M. Boqueras* A88 Dupl. (BCC 4927).

10. **Leptorhaphis parameca** (Massal.) Körber, *Parerg. lich.*: 386 (1865). *Sagedia (Campylacia) parameca* Massal., *Symm. lich.*: 97 (1855). *Spermatodium paramecum* (Massal.) Trevisan, *Conspec. verruc.*: 12 (1860). *Verrucaria parameca* (Massal.) Stizenb. in *Jahrb. St. Gall. Naturw. Ges.* **22**: 513 (1882) ['1880–1881']. Type: Italy, Verona, 'ad truncos *Pruni mahleb*', *A. B. Massalongo* (VER!—holotype; BM! isotype).

?*Endophis cerasi* Norman in *Nyt Magaz. Naturvid.* **7**: 240 (1853).

Leptorhaphis xylographoides Norman in *Ofvers. K. VetenksAkad. Förh. Stockh.* **41**(8): 40 (1884). Type: Norway, Akersus, Asker parochia, between Raunborg and

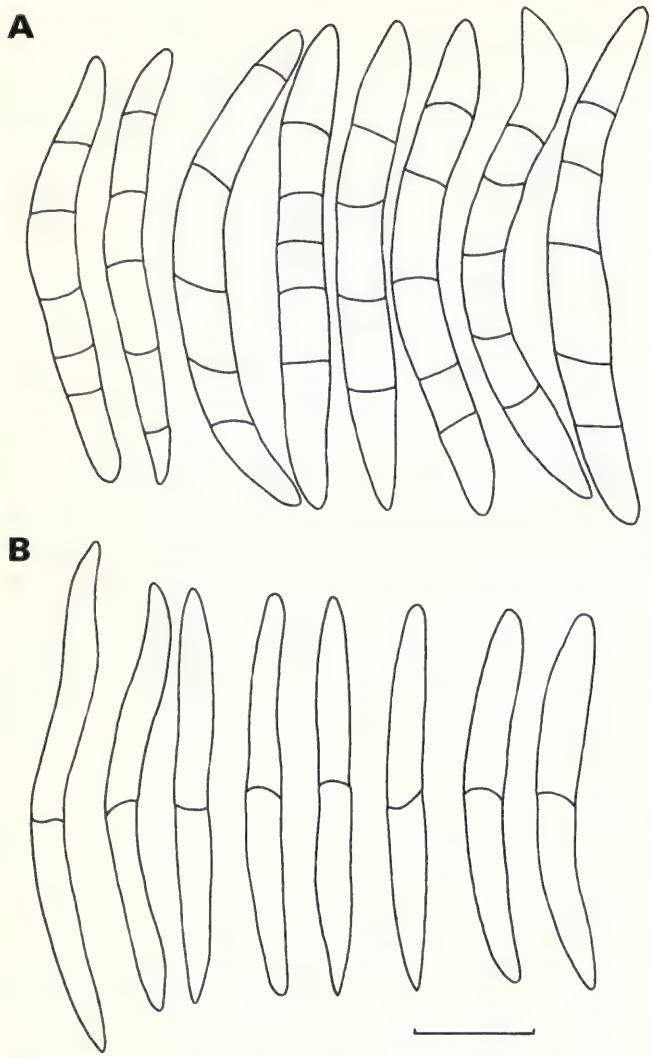


Fig. 16 Ascospore outlines (A) *Leptorhaphis oleae* (Massal.) Körber (VER–holotype); (B) *Leptorhaphis parameca* (Massal.) Körber (VER–holotype); scale = 10 μm.

Asker, on *Prunus avium*, *J. M. Norman* ['*Endophis cerasi*' bonat. praemiss.] (O!—lectotype, selected here; UPS!—isolectotype).

Fig. 16B, 17.

Thallus: Inconspicuous; immersed in the substratum, consisting of dark brown to greenish-black, smooth, thin-walled hyphae, *c.* 4 μm wide, constricted at the septa; presumably not lichenized.

Ascomata: Black, smooth, shiny, ellipsoidal, *c.* 285–365 μm diam; immersed in the bark, becoming superficial, dimidiate, hemispherical to applanate, 90–110 μm high, slightly mammiform; ostiole centrally located in a small depression. Involucrellum: greenish-black, *c.* 15–18 μm thick, covering the exciple and extending beyond the ascomata in a basal fringe, 170–300 μm wide; composed of radiating dark brown, smooth, thin-walled hyphae, *c.* 4 μm wide, intermixed with bark cells forming a clypeus of textura intricata, becoming in places a pseudoparenchymatic tissue of leptodermatous cells. Exciple: surrounding the centrum, consisting of colourless to pale brown and isodiametric cells forming a textura angularis. Hamathecium: of pseudoparaphyses, *c.* 2–2.5 μm wide; hymenial gelatin bluish in iodine. Asci: cylindrical-clavate, short and broad- stalked, 45–70 × 13–17 μm; with two functional wall layers, the outer thin and smooth, the inner thicker, with a broad and truncate apex, slightly indented; 8-spored. Ascospores: arranged in one or two bundles in the asci, sometimes helically twisted, fusiform, arcuate or sigmoid, 30–45 × 3–4 μm, 1-septate, apices attenuated.

Conidiomata: Not observed.

ECOLOGY. On bare bark of different species of *Prunus*, such as *P. avium* (L.) L. and *P. cerasus* L.; a saprobe, not causing any apparent damage.

DISTRIBUTION. Europe, known from Italy, Germany, Switzerland, and Norway; North America, known from North Carolina and Michigan; probably common on *Prunus* bark, but overlooked due to its small size.

TYPIFICATION. Two type collections of *Sagedia parameca* were located at VER and BM. Material from Massalongo's herbarium in VER is here regared as the holotype, while the material from BM remains as an isotype. The lectotype of *Leptorhaphis xylographoides* is here selected from Norman's herbarium at O, while the material from UPS remains as an isolectotype, although ascomata were more abundant in the latter. A second isolectotype from Norman's herbarium in O, borrowed by Keissler in 1932, is now missing.

OBSERVATIONS. Harris (1973: 23) regarded *Leptorhaphis contorta* as perhaps not distinct from *L. parameca*. Nevertheless several features, like presence of basal fringe, bluish iodine reaction, broad and truncate ascus apex, and smaller ascospore length: breadth ratio, are sufficient to distinguish both taxa. Moreover *L. contorta* seems at present restricted to northern America and Iceland, whereas *L. parameca*'s distribution, although scattered, is more widespread in the Northern Hemisphere.

ADDITIONAL SPECIMENS. **Austria**, Südl. Württemberg, Egg momnoried, near Wurzech, on *Prunus*, *Herter* (B 59699). **Italy**, Tirolo Meridionale, Bolzano, Ritten Mountain, 'sul *Prunus avium* selvatico', *F. Hausmann* [*Erb. Critt. Ital. ser. I exs.* no. 121 (1121), as *Sagedia parameca* Massal.] (BM, B 59700). [Sine loc.], *M. Anzi* (B 59596). **West Germany**, Oberbayern, Voralpen, Benedictbeuern, *c.* 700m, on *Prunus cerasus*, 28 June 1902, *G. Lettau* (B 59701). **Switzerland**, Zürich, Zürichberge, 'an der Rinde eines junger Kirschbaumes Walde', December 1876, *H. G. Winter* [Arnold, *Lich. exs.* no. 726, as *Leptorhaphis parameca*] (BM, PC, B 59696). Geneva, Salève, 'sur cerasus', *J. Müller* (PC). Weugen, Weugwald, 'Kirschbaum', 19 July 1929, *V. J. Grummann* (B 59695). **USA**, Michigan, Alger County, North of Kingston Lake, on *Prunus* in open fields and woods, 4 September 1965, *R. C. Harris* (BM). North Carolina, Great Smoky Mountains, Mt. Kephart, *c.* 1790m, on *Prunus pensylvanica*, 15 September 1939, *G. Degelius* (herb. Degelius).

11. **Leptorhaphis psilotera** (Nyl.) Arnold in *Flora, Jena* **68**: 164 (1885). *Verrucaria psilotera* Nyl. in *Flora, Jena* **58**: 14 (1875). *Leptorhaphis oxyspora* var. *psilotera* (Nyl.) Blomb. & Fors., *Enumer. Plant. Scandinaviae*: 106 (1880). *Campylacia psilotera* (Nyl.) Vainio in *Acta Soc. Fauna Flora fenn.* **49**(2): 190 (1921). Type: Finland, Tavastia australis, Luhanka, Vahermäki, on bark of *Daphne*, 1873, *E. Lang* (= Vainio) (H-NYL 630!—lectotype, selected here; NYL 329!—isolectotype).

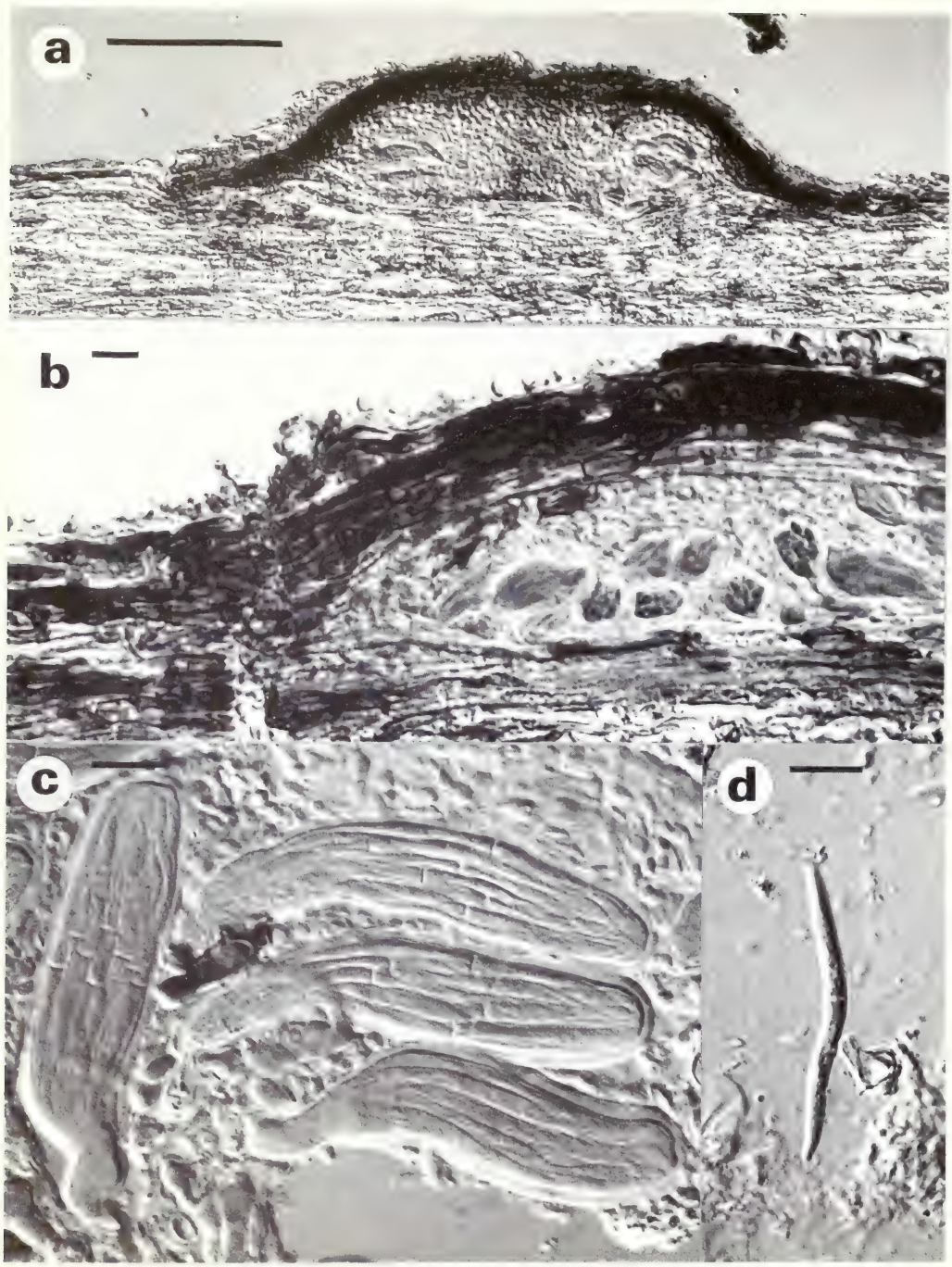


Fig. 17 *Leptorhaphis parameca* (Massal.) Körber (VER–holotype) (a) Vertical section of ascoma showing basal fringe; scale = 100 μm; (b) Detail of involucrellum (vertical section): clypeus; (c) Asci, ascospores and pseudoparaphyses; (d) Ascospore; scale = 10 μm.

Fig. 18, 19.

Thallus: Inconspicuous to greenish grey.

Ascomata: Black, shiny, smooth, somewhat circular, 150–200 μm diam, not surrounded by a basal fringe; immersed in the substratum, becoming half immersed to superficial, hemispherical to applanate, mammiform, *c.* 65 μm in height; ostiole centrally located in a small depression. Involucrellum: greenish-black, *c.* 20 μm thick, not extending beyond in a basal fringe; consisting of bark material mixed with dark brown to greenish-black, smooth, thin-walled hyphae, *c.* 3 μm wide, forming a clypeus of elongated radiating cells of textura intricata, becoming in places a pseudoparenchymatous tissue of leptodermatous cells. Exciple: almost indistinct, very narrow, consisting of colourless, thin-walled, smooth, isodiametric cells, formimg a textura globulosa to angularis, radially compressed at the bottom of the ascomatal cavity. Hamathecium: consisting of pseudoparaphyses, *c.* 1.5–2 μm

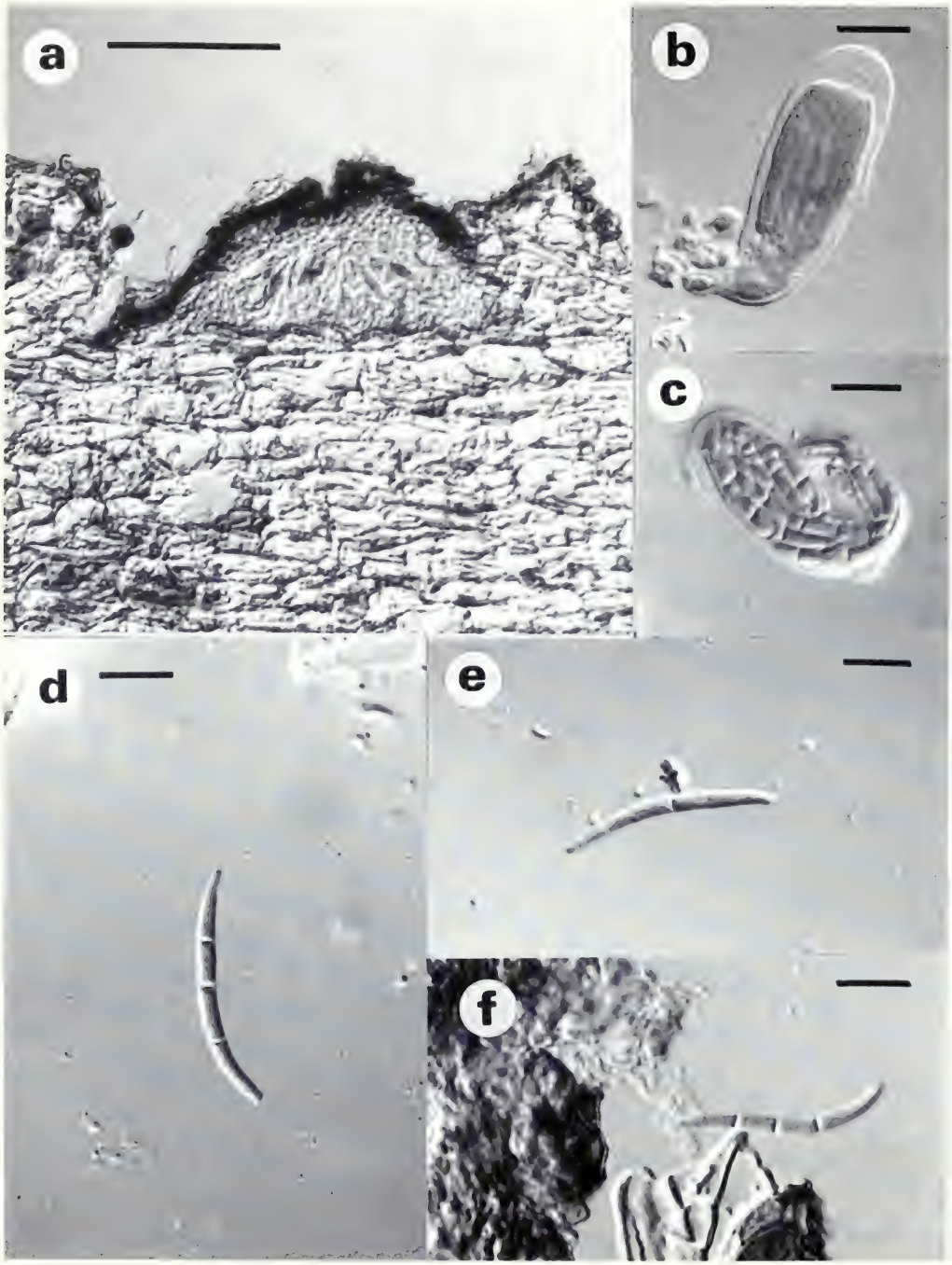


Fig. 18 *Leptorhaphis psilotera* (Nyl.) Arnold (H-NYL 629) (a) Vertical section of ascoma; scale = 100 µm; (b), (c) Asci and ascospores; (d), (e), (f) Ascospores; scale = 10 µm.

wide; hymenial gelatin bluish in iodine. Asci: cylindrical-clavate, short and broad-stalked, 50–60 × 7–11 µm; with two functional wall layers, the outer thin and smooth, the inner thicker, especially at the apex, which is broad and truncate; 8-spored. Ascospores: arranged in one or two bundles in the asci, sometimes helically twisted, narrowly fusiform, sigmoid, (35–) 40–55 × 2–3 µm, 1–, 3-septate, attenuated at the apices.

Conidiomata: Not observed.

ECOLOGY. On bare bark of *Daphne mezereum* L. and *Salix*, not causing any apparent damage, presumably saprophytic.

DISTRIBUTION. Europe; known only from Scandinavia.

TYPIFICATION. The type material of the species was originally a mixed collection from Norland (Norway) and Tavastia (Finland), collected on *Salix* and *Daphne* respectively. From the specimens originally collected in Finland, H-NYL 630 on bark of *Daphne* is here selected as the lectotype, since the

name of the species plus other details like ascospores measurements were handwritten by Nylander on the packet in red ink. This is presumably the specimen used by Nylander to prepare the species diagnosis.

OBSERVATIONS. As mentioned above, two different collections of this species are known from Scandinavia. Studies of the material revealed that the specimen from Norway, on *Salix* bark, has smaller ascus and ascospore size (25–40 × 2–3 µm), with also smaller ascospore length: breadth ratio (10–15:1). Both collections present a rather similar ascospore morphology, suggesting that they are probably related. Moreover Vainio's (1921: 190) ascospore measuments of the species collected in Finland on *Daphne* bark, are slightly smaller (30–40 × 1.5–2 µm) than my own measurements of the same species in lactophenol cotton-blue. Therefore at present both species are kept together, until more material of the species on *Salix* bark becomes available.

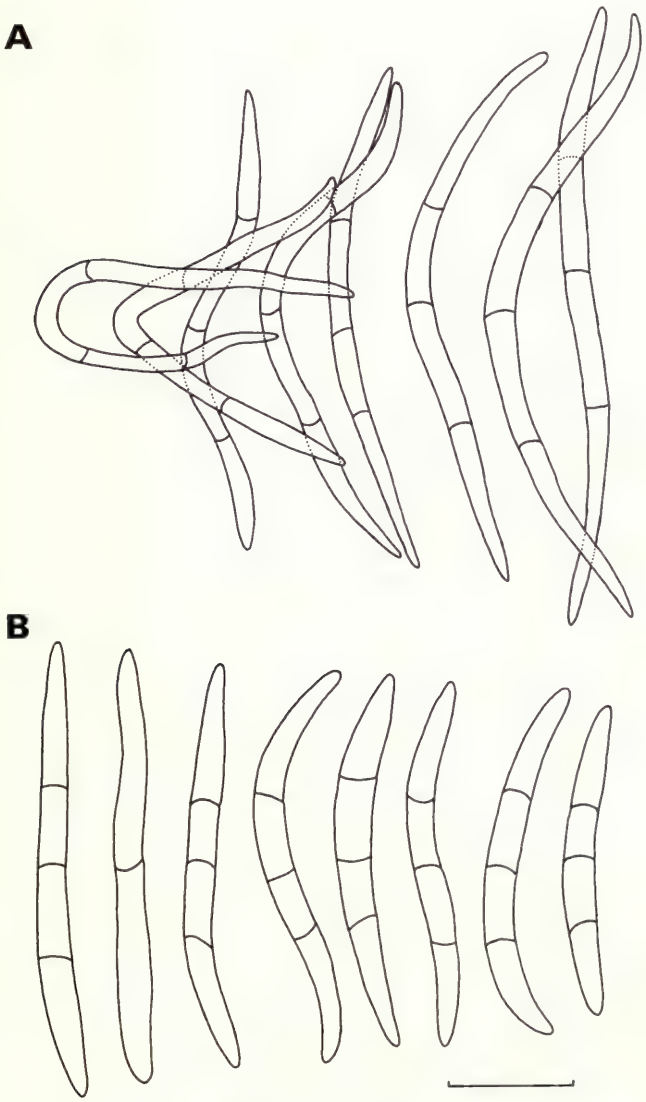


Fig. 19 Ascospore outlines of *Leptorhaphis psilotera* (Nyl.) Arnold (A) H-NYL 630–lectotype; (B) H–NYL 629; scale = 10 µm.

On ascospore morphology *Leptorhaphis psilotera* could be mistaken for *L. contorta* or *L. parameca*. It differs from the latter in its coloured iodine reaction of the hymenial gelatin, as well as in its ascus apex morphology, slightly pointed in *L. contorta*. On the other hand, both *L. parameca* and *L. psilotera* have bluish iodine reaction, but the shape of the ascomata and the presence of a characteristic basal fringe in *L. parameca* distinguish it from the latter.

ADDITIONAL SPECIMENS. **Finland**, Kankaanpää, Venesjärvi, Sinahmi, Jokilahti, 'ad corticem *Daphnis mezerei* in loco pascuo', 6 August 1935, *M. Laurila* (H). **Norway**, Nordland, Bodöen, on *Salix* sp., 1868, *J. E. Zetterstedt* (H-NYL 629).

12. **Leptorhaphis tremulae** Körber, *Syst. lich. Germ.*: 372 (1855). *Campylacia tremulae* (Körber) Massal., *Sched. Critic.*: 184 (1856). *Verrucaria oxyspora* var. *tremulae* (Körber) Nyl. in *Not. Sällsk. Fauna Fl. fenn. Förhandl.* **1**: 7 (1858). *Pyrenula tremulae* (Körber) Hepp, *Flecht. Eur. exs.* no. 706 (1860). *Spermatodium tremulae* (Körber) Trevisan, *Conspec. verruc.*: 12 (1860). *Arthopyrenia tremulae* (Körber) Müll. Arg. in *Mém. Soc. phys. Hist. nat. Genève* **16**: 430 (1862). *Sagedia tremulae* (Körber) Anzi in *Atti Soc. Ital. Sci. nat.* **9**: 257 (1866). *Verrucaria epidermidis* var. *tremulae* (Körber) P. Crouan & H. Crouan, Fl. Finist.: 87 (1867). *Arthopyrenia oxyspora* var. *tremulae* (Körber) H. Olivier, *Flora Lich. Orne*: 273 (1884). *Verrucaria tremulae* (Körber) Harm. in *Bull. Soc. Sci. Nancy* II, **34**: 91 (1900) ['1889']. *Mycoleptorhaphis tremulae* (Körber) Cif. & Tom. in *Atti Ist. bot. Univ. Pavia* V, **10**: 258 (1954). Type: Poland, Silesia, ... [illegible], on *Populus dilatata*, 29 May 1840, *'W. U. Chauisé'* (L!—lectotype, selected here; WRSL!—isolectotype).

Verrucaria sphenospora Nyl. in *Flora, Jena* **52**: 412 (1869). *Leptorhaphis sphenospora* (Nyl.) Arnold in *Flora, Jena* **53**: 484 (1870). *Campylacia sphenospora* (Nyl.) Vainio in *Acta Soc. Fauna Flora fenn.* **49**(2): 190 (1921). *Leptorhaphis tremulae* var. *sphenospora* (Nyl.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1(2): 258 (1938). Type: Finland, Ostrobottnia borealis, Lappi, Ylitornio, 'Lapponia, Alkkula', on *Populus* branches, 1867, *J. P. Norrlin* (H-NYL 730!—lectotype, selected here; H-NYL 7500!, H!, BM!—isolectotypes).

Fig. 20, 21.

Thallus: Inconspicuous; immersed in the substratum, composed of colourless, smooth, thin-walled hyphae, less than 3 µm wide, constricted at the septa; not associated with algae.

Ascomata: Black, matt, smooth, numerous, scattered singly, circular, *c.* 135–250 µm diam; immersed in the substratum, becoming superficial, hemispherical to applanate, dimidiate, *c.* 55–75 µm tall; ostiole centrally located. Involucrellum: dark-brown to greenish-black, *c.* 10–15 µm thick, covering the centrum, extending in a basal fringe, *c.* 55 µm long; composed of bark material intermixed with greenish-black to dark brown, smooth, thin-walled hyphae, constricted at the septa, not changing colour in KOH, forming a clypeus of textura epidermoidea-intricata. Exciple: not differentiated. Hamathecium : of pseudoparaphyses, *c.* 2–2.5 µm broad; hymenial gelatin not changing colour in iodine. Asci: scarce, ovoid-clavate, ventricose, short-stalked, 40–66 × 18–25 µm; with two functional wall layers, the outer thin and smooth, the inner thicker at the tip, with a broad and truncate internal apical beak, slightly indented; 8- to 16-spored. Ascospores: arranged in two or three bundles in the asci, colourless,

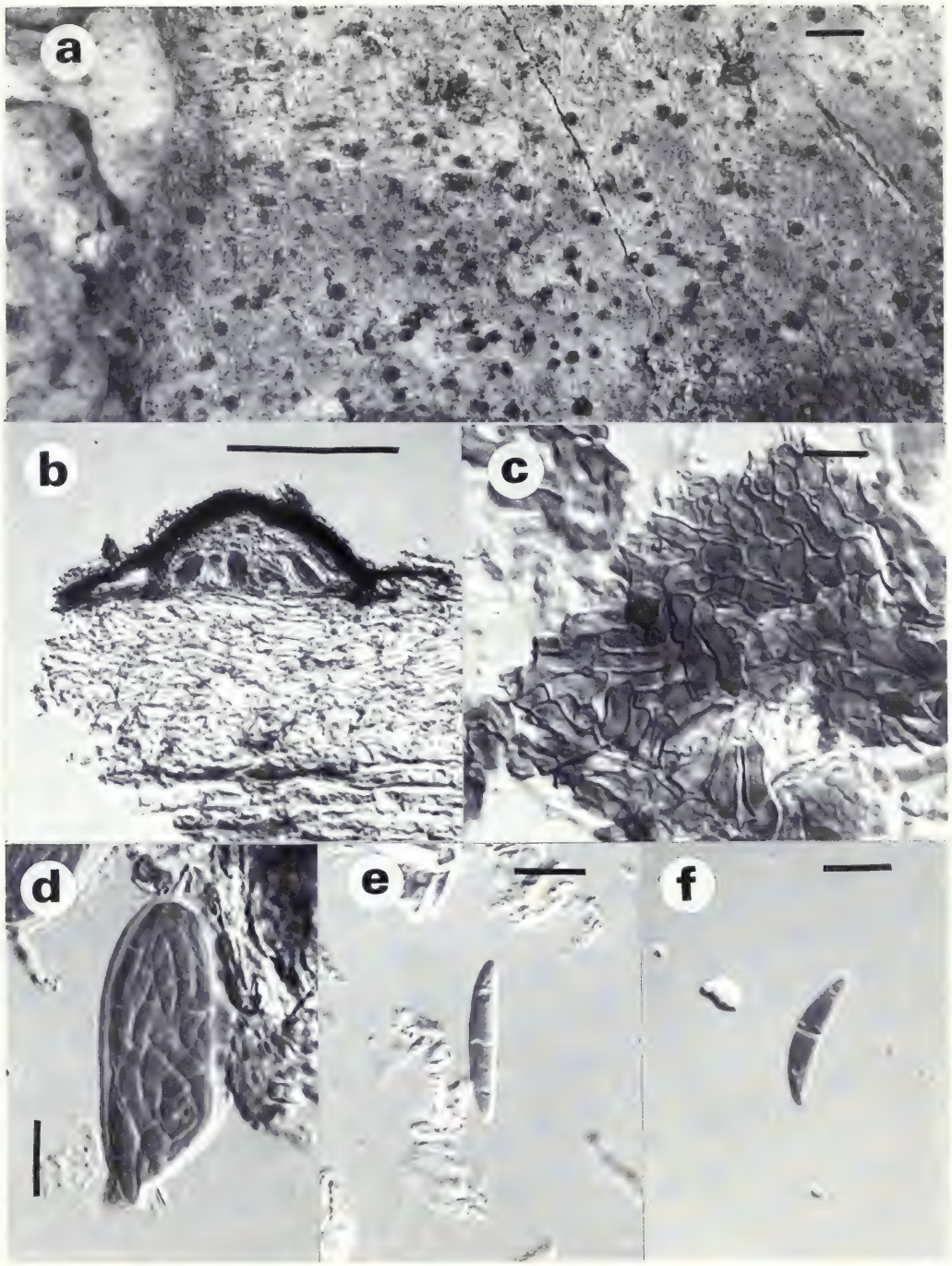


Fig. 20 *Leptorhaphis tremulae* Körber (L–lectotype) (a) Surface view; scale = 500 μm; (b) Vertical section of ascoma; scale = 100 μm; (c) Detail of involucrellum (surface view): textura epidermoidea-intricata; (d) 16-spored asci; (e), (f) Ascospores; scale = 10 μm.

smooth, thin-walled, fusiform, arcuate, 13–25.5 × 3–4.5 μm, 1-septate, with rounded apices.

Conidiomata: Not observed.

ECOLOGY. Mainly on twigs and branches of *Populus* species, e.g. *P. nigra* L., and *P. alba* L., as saprobes, not causing any apparent damage.

DISTRIBUTION. Known from central and northern Europe: Poland, Germany, France, and Finland, in the middle of the last century; I am not aware of any recent records.

TYPIFICATION. The specific epithet *'tremulae'* has been the origin of confusion since its first application by Körber (1855: 372) to two species of *Leptorhaphis* occurring on *Populus* bark: *L. tremulae* and *L. atomaria*. The author based his description on two different specimens: *V. stigmatella* var. *tremulae* Flörke. (in herb. Günth.) and *Verrucaria*

epidermidis var. *lunulata* Flotow, as a result of which he described a fungus with a cinereous to dark thallus, 6-, 8-spored asci, and 1-, 3-septate, acicular-fusiform ascospores; this conforms to the species concept of *L. atomaria*.

According to Vainio (1921: 189), an original collection of *Verrucaria stigmatella* var. *tremulae* Ach. proved to be a facultative synonym of *Lichen atomarius* Ach. [i.e. *Leptorhaphis atomaria* (Ach.) Szat.], whereas a second specimen from Sweden, *Verrucaria tremulae* Ach. is probably the pycnidial state of *Lecidea glomerulosa* (DC.) Steud. [i.e. *Lecidella euphorea* (Flk.) Hertel]. However, type material of *V. stigmatella* var. *tremulae* obtained from Helsinki (H-ACH 778) is a mixed collection with several pieces of bark, only one of which is labelled 'Suecia', containing ascomata and conidiomata of a lecideoid fungus, presumably *Lecidea glomerulosa* as stated by Vainio, but no material related to *Leptorhaphis tremulae* or *L. atomaria*. *Verrucaria stigmatella* var. *tremulae* Ach. is also represented at BM-ACH 286. The collection consists of two pieces of bark, neither of which contains fungal material related to *Leptorhaphis*. The biggest piece of bark (no.7), presumably *Populus tremula*, is covered by a lecideaceous fungus bearing small pycnidia, and the smallest (no.6), an unidentified piece of bark, contains a species referrable to *Anisomeridium*, probably *A. biforme* (Borrer.) Harris.

Herbarium material referred to as *Verrucaria stigmatella* var. *tremulae* Flörke was not located among the specimens studied from L or WRSL. However, the study of the original material of *Verrucaria epidermidis* var. *lunulata* from WRSL and L Körber's general herbarium, and Körber *Lich. Sel. Germ. exs.* no. 119 (1856) from L, revealed a fungus with polyspored asci (16-spored), and smaller, 1-septate, acicular ascospores, which in my opinion should be regarded as falling within the species concept of *L. tremulae*. Material of *Verrucaria epidermidis* var. *lunulata* from Körber's general herbarium (L) is here selected as lectotype, and thus recognized as a different species from *L. atomaria*, and crediting the epithet '*tremulae*' only to Körber.

Several isotype collections of *Verrucaria sphenospora* Nyl. have been obtained from H and BM. H-NYL 730 is here selected as lectotype since it is in particularly good condition and is one of the specimens originally kept in Nylander's herbarium.

OBSERVATIONS. This species differs from *Leptorhaphis atomaria* and *L. lucida*, also described on *Populus* bark, in its polyspored asci, negative iodine reaction, and smaller ascospores. Furthermore, the species occupies a different habitat on the bark of *Populus*, since it is commom on branches and twigs, whereas *L. atomaria* and *L. lucida* occur on the trunks.

Although the specimens examined did not contain conidiomata, Harris (in litt.) observed macroconidia, similar in shape to the ascospores and *c.* 10–11 × 1.5–2.5 µm, in a specimen kept in NY of Hepp *Lich. Helvet.* exs. no. 706.

ADDITIONAL SPECIMENS. France, Saline, 'branches de peupliers', 26 January 1899, *E. Moncuillon* (BM). **West Germany**, Henssen, Marburg, on bark of *Populus nigra*, 1858, *W. Uloth* [Hepp, *Lich. Helvet. exs.* no. 706, as *Pyrenula tremulae*] (L, PC-HUE 3505/2, BM, E). Bayern, Eichstätt, Wiesengässchen, on branches of *Populus pyramidalis*, Spring 1878, *Boll* (BM; B 59600). Nordrhein-Westfalen, Greven, on *Populus dilatata*, August 1862, *W. Fuiting* (B 59594). **Poland**, Silesia, Hirschbergam, trunks of *Populus dilatata*, 1856, *G.W. Körber*

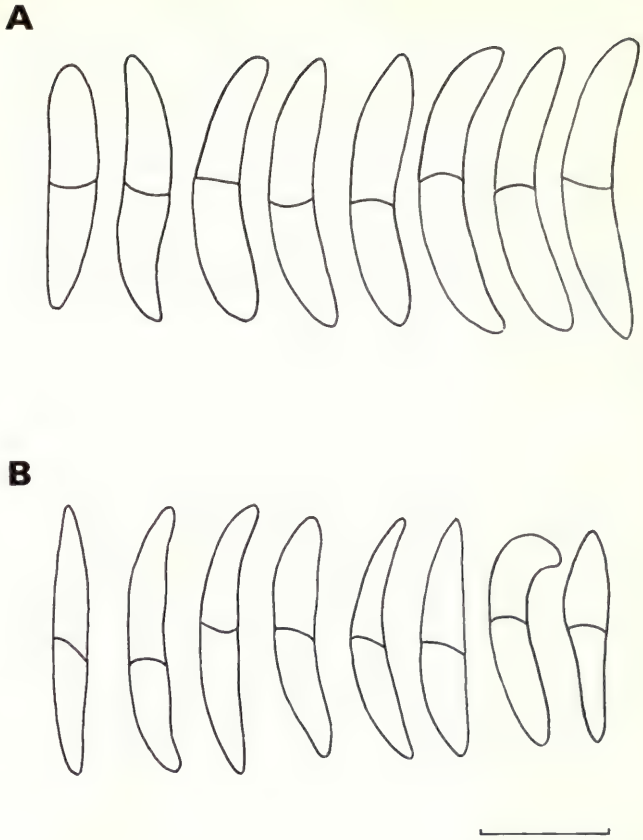


Fig. 21 Ascospore outlines of *Leptorhaphis tremulae* Körber (A) H-NYL 730–lectotype of *Verrucaria sphenospora*; (B) L–lectotype & WRSL–isolectotype of *Leptorhaphis tremulae*; scale = 10 µm.

[Körber, *Lich. Sel. Germ. exs.* no. 119, as *Leptorhaphis tremulae*] (L; B 59612).

II. **Arthopyrenia** Massal.

Arthopyrenia Massal., *Richerch. Auton. lich.*: 165 (1852). Type species: *Verrucaria rhyponta* Ach. [*Arthopyrenia rhyponta* (Ach.) Massal.] (lectotype proposed by Riedl, 1962: 265). [See Harris, 1975: 35, for generic synonyms].

Thallus: Inconspicuous, or greyish, brownish to olivaceous-black, smooth, matt, continuous, but not delimited by a prothallus; superficial to endophloedal; composed of colourless to dark brown or greenish-black, smooth, thin-walled hyphae, septate, constricted at the septa, sometimes associated with trentepohlioid algae.

Ascomata: Perithecioid, dark brown to black, shiny, smooth, numerous, scattered singly, circular to somewhat ellipsoidal; immersed in the substratum to superficial, hemispherical to applanate, sometimes mammiform, dimidiate; ostiole centrally located in a small depression. Involucrellum: consisting of dark brown or greenish-black hyphae, sometimes becoming olivaceous or greenish in 10% KOH solution, intermixed with bark material, forming a clypeate tissue of textura intricata to epidermoidea, becoming in places a pseudoparenchymatic tissue of leptodermatous cells. Exciple: colourless to pale brown, often intergrading with the involucrellum; consisting of smooth, thin-walled, isodiametric cells, forming a pseudoparenchymatous tissue of leptodermatous or mesodermatous cells; sometimes not differentiated.

Hamathecium: of pseudoparaphyses, composed of colourless, thin-walled, cellular, branching and anastomosing hyphae, constricted at the septa, forming a compact net enveloped in mucus; periphyses or periphysoids not observed; hymenial gelatin not changing colour in iodine, sometimes yellowish-amber or bluish, but never deep blue. Asci: arising from the base and angles of the ascomata cavity, ripening sequentially, cylindrical to ovate, short-stalked; with two functional layers, the outer thin and smooth, the inner thicker towards the apex, with a narrow and pointed internal apical beak, not changing colour in iodine; no other apical structures seen; 8-spored; discharge fissitunicate. Ascospores: biseriately or irregularly arranged in the asci, colourless or rarely pale brown, narrowly ovate, 1-, 3-septate, slightly constricted at the septa, cells usually somewhat unequal, with an attenuated lower cell; sometimes the cells become slightly constricted medially but without a true septum, with a somewhat thick epispore, smooth or rarely finely ornamented, gelatinous sheaths sometimes present, swelling considerably in water and KOH.

Conidiomata: When present, pycnidial, blackish, shiny, smooth, scattered singly, circular; immersed in the substratum to superficial, globose, with a central ostiole. Wall: dark brown nearly black, consisting of isodiametric cells, with dark brown, smooth, more or less thick walls and enlarged lumen, forming a pseudoparenchymatous tissue, sometimes intermixed with bark material forming a clypeus of textura intricata. Conidiogenesis: presumably enteroblastic. Conidiogenous cells: colourless, thin-walled, smooth, lageniform-ampulliform, arising from colourless, thin-walled isodiametric cells adjacent to the wall. Macroconidia: narrowly ovate and septate like the ascospores. Microconidia: colourless, aseptate, thin-walled, smooth, bacilliform, globose or subglobose, without appendages or gelatinous sheaths.

NUMBER OF SPECIES. Zahlbruckner (1921–22, 1932) listed over 200 taxa which had been referred to *Arthopyrenia* on the basis of ascospore morphology and colour, but as a result the genus was an unnatural assemblage. Harris (1975), in a critical taxonomic study of the North American species, transferred many taxa to different genera, often belonging to different families and orders. He also delimited the generic concept as given above, and recognized the members of the genus on the basis of their ascolocular ascomata, not developing a pseudostromata, pseudoparaphyses branched and anastomosed, sometimes gelatinized, cylindrical to ovate asci with a narrow and pointed internal apical beak, 8-spored, colourless to pale brown, narrowly ovate ascospores, 1-, 3-septate, spore wall sometimes ornamented and the gelatinous sheath usually well developed. Additional characteristics such as the hymenial gelatin iodine reaction or colour change of the hyphae of the involucrellum in 10% KOH solution could be also used to distinguish species within the genus.

ECOLOGY. In the Northern Hemisphere generally growing on smooth, young bark of deciduous trees, shrubs, and conifers. Harris (1975: 38) accepted the genus as non-lichenized and to some extent parasitic, since the hyphae might well be able to invade living tissues. Nevertheless, he found that some populations of primarily non-lichenized species can be regularly associated with trentepohlioid algae. Some other species are lichenicolous (David, 1986). The species are usually characteristic of pioneer lichen communities.

DISTRIBUTION. Reportedly cosmopolitan, but many of the tropical taxa included in the genus should perhaps be referred elsewhere (see Harris, 1975).

TYPIFICATION AND NOMENCLATURE. Harris (1975: 37) accepted Riedl's lectotypification of the genus, but this requires regulation by conservation (Hawksworth, 1985*a*: 133, 134). The earlier typification with *Arthopyrenia analepta* (Ach.) Massal. by Th. Fries (1861: 111) is based on *Lichen analeptus* Ach. a name of uncertain application (see Hawksworth, 1985*a*: 133). A second typification by Clements & Shear (1931: 288) was also rejected on the basis that the species selected, *A. pyrenuloides* (Fée) Müll. Arg., was not included among the original species described by Massalongo (1852: 165–170).

RELATIONSHIPS. Riedl (1962: 263) included the genus *Arthopyrenia* and correlated genera like *Leptorhaphis* among the Mycoporaceae Zahlbr., which has nomenclatural priority over the Dermatinaceae Hillm. In his opinion the Arthopyreniaceae cannot be separated from the Mycoporoceae on the basis of characteristics such as the presence of plurilocular ascomata, which are not sufficient to recognize two families.

Eriksson (1981: 30) however preferred to maintain the Arthopyreniaceae, since both families also differ in hamathecial development, as a result of which the Arthopyreniaceae has pseudoparaphyses and Mycoporaceae net-like paraphysoids. He also rejected the emplacement of *Arthopyrenia* among the Pleosporaceae, as proposed by Poelt (1974: 607) and Harris (1975: 34), on the basis of differences in ascus morphology, ascomata and anamorphs.

OBSERVATIONS. The following taxa were unfortunately referred to *Leptorhaphis* by Magnusson (1936), presumably because the ascospores were described as narrowly shaped as in *A. stenospora*, or more than 1-septate, as in *A. pithyophila*. This treatment was also accepted by Santesson (1984). For the time being these are treated as separate taxa, although they might prove to be synonymous with other taxa already described in *Arthopyrenia*, as in the case of *A. stenospora*, discussed below (p. 128), which I found to be closely related to material referred to *A. punctiformis* s. lat., although type material of the latter was not studied.

The species

1. **Arthopyrenia olivatra** Norman in *Ofvers. K. VetenskAkad. Förh. Stockh.* **41**(8): 38 (1885) ['1884']. *Leptorhaphis olivatra* (Norman) Magnusson in *Förteckn. Skandinaviens Växter* **4**: 10 (1936). Type: Norway, Bergen, Isladen, on *Alnus glutinosa*, *J. M. Norman* (O!–holotype).

Fig. 22, 23A.

Thallus: Olivaceous brown, nearly black, thin and smooth to slightly furrowed, matt, continuous, but not surrounded by an hypothallus; superficial to endophloedal, superficially composed of greenish-black, thin-walled, smooth hyphae, *c.* 3.5–5.5 µm wide, constricted at the septa, becoming hyaline and thinner when immersed in the bark; not associated with algal cells.

Ascomata: Blackish, shiny, smooth, scattered singly, circular to ellipsoidal, 150–250 µm diam; immersed in the substratum, becoming superficial, hemispherical to applanate, *c.* 100 µm in height; ostiole centrally located in a small depression. Involucrellum: dark brown, *c.* 30 µm thick, consisting of a clypeus composed of bark material intermixed with greenish-black, thin-walled and smooth hyphae, *c.* 5 µm

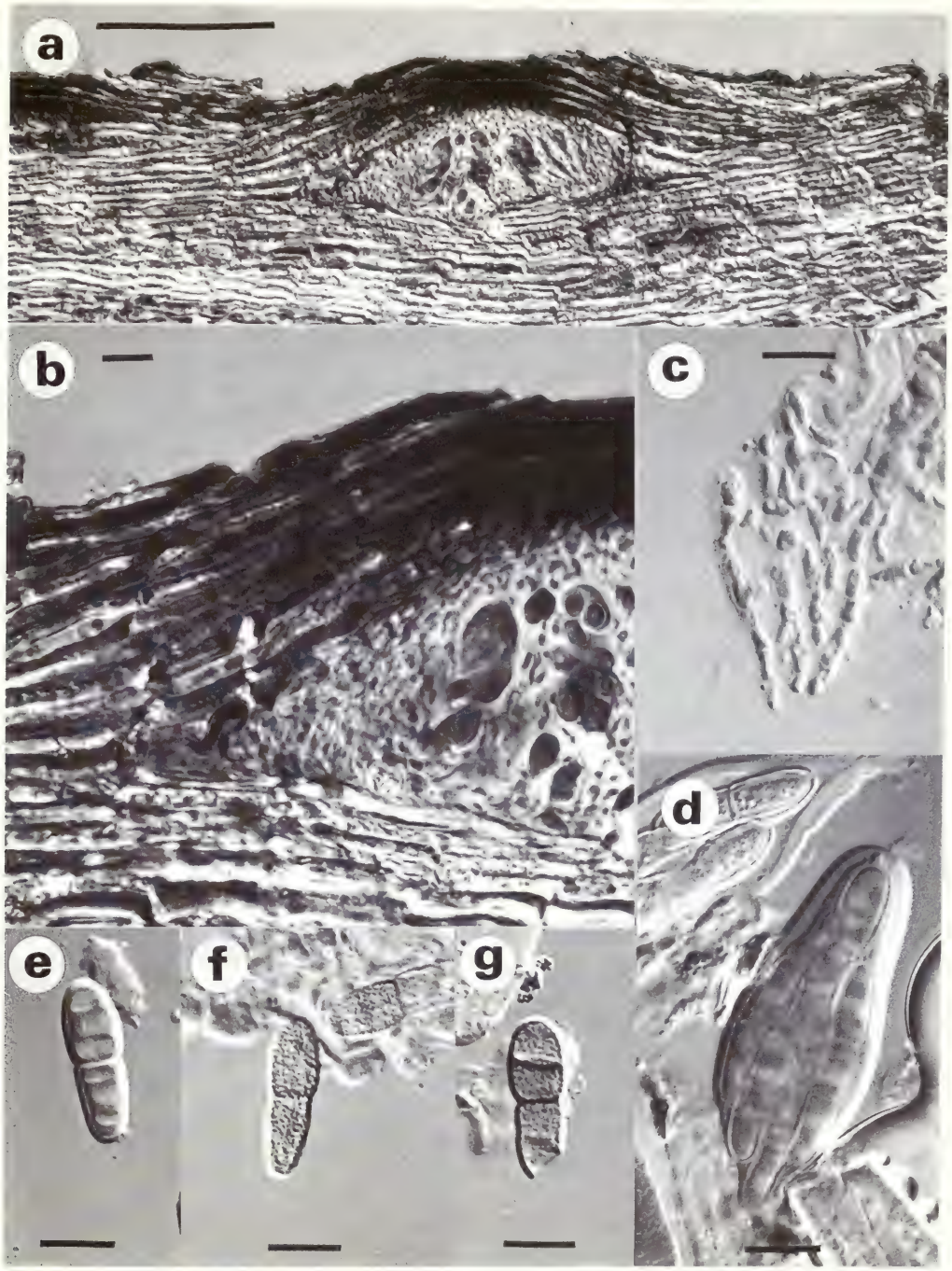


Fig. 22 *Arthopyrenia olivatra* Norman (O–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of involucrellum (vertical section): clypeus; (c) Pseudoparaphyses; (d) Ascus and ascospores; (e) Young ascospore, 1-septate; (f), (g) Mature ascospores: pigmentation, ornamentation, 3-septate; scale = 10 μm.

thick, constricted at the septa, forming a textura intricata, becoming in places a pseudoparenchymatic tissue of isodiametric and thin-walled cells. Exciple: not differentiated. Hamathecium: of pseudoparaphyses, *c.* 2–2.5 μm wide; hymenial gelatin not changing colour in iodine. Asci: scanty, cylindrical- ovate, short-stalked, 50–60 × 17–20 μm, with two functional wall layers, the outer thin and smooth and the inner wall becoming thicker at the apex, with a long and narrow internal apical beak; 8-spored. Ascospores: irregularly arranged in the ascus, colourless, becoming brown when mature, epispore thick, indistinctly verruculose, narrowly ovate, 18.5–23 × 5–8 μm, 1- to 3-septate, only constricted at the middle septum, with somewhat unequal cells, the lower narrower and smaller, with 2–3 refringent particles in each cell, without differentiated gelatinous perispore.

Conidiomata: Not observed.

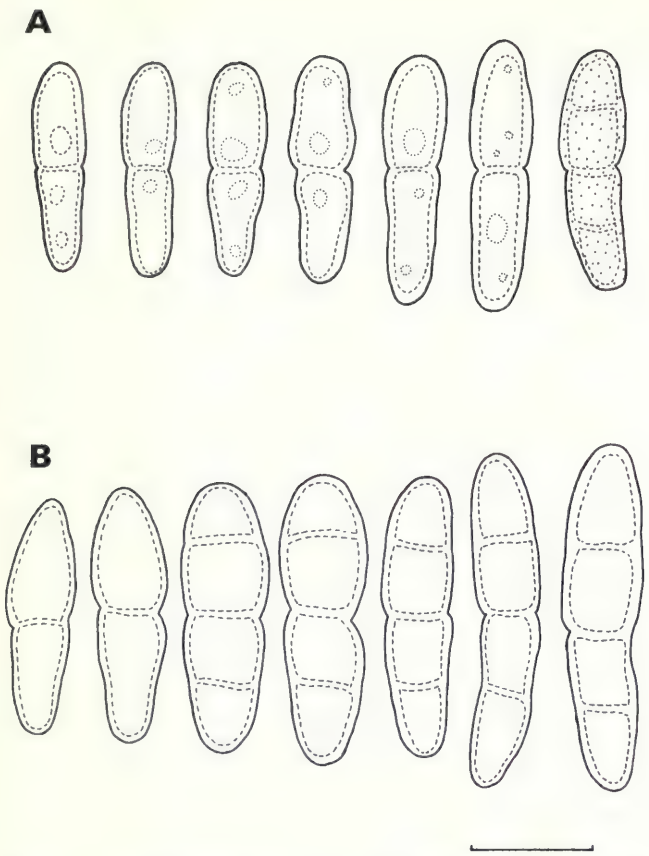


Fig. 23 Ascospore outlines (A) *Arthopyrenia olivatra* Norman (O–holotype); (B) *Arthopyrenia pithyophila* Th. Fr. & Blomb. (LD–holotype); scale = 10 μm.

ECOLOGY. On smooth bark of *Alnus glutinosa* (L.) Gaertner, forming dark patches, presumably not lichenized, but not causing apparent damage.

DISTRIBUTION. Europe, Scandinavia, Norway; known only from the type locality in Bergen, and from Sörhalt, probably with a wider distribution in temperate regions, but overlooked.

TYPIFICATION. Only one collection of the species from the type locality was located at Norman's herbarium in O, which is therefore accepted as the holotype.

OBSERVATIONS. This taxon resembles superficially another *Arthopyrenia* species included here: *A. umbripicta*, both having olivaceous brown to black thalli. Nevertheless *A. olivatra* has slightly larger asci and ascospores, which become 3-septate, with brownish and verruculose walls when mature.

Arthopyrenia rhyponta (Ach.) Massal. is perhaps closely related to *A. olivatra*, since it also has a dark thallus, consisting of thick dark brown hyphae, 3-septate ascospores, and similar ascospore and ascus sizes (Harris, 1975: 66), but I have not studied type or original material of the species. A second species, *A. lyrata*, described by Harris (1975: 72) as having 1-septate ascospores, which become 3-septate when mature, and ornamented ascospore walls, may be related to *A. olivatra*, although Harris considered the taxon as belonging to a different group within *Arthopyrenia* on the basis of its slender, thread-like paraphyses and ascospore wall morphology, with a thick wall, forming a partial subdivision of the spore lumen, and thick perispore. However, these characteristics were not observed in *A. olivatra*.

At present the taxon is treated as a separate species, although it might prove to be a synonym of some other European taxa, already described in *Arthopyrenia*, but not treated in Harris' (1975) taxonomic revision.

ADDITIONAL SPECIMENS. **Norway**, Sörhalt paroch., 'Grskang', 1877, *J. M. Norman* (O).

2. **Arthopyrenia pithyophila** Th. Fr. & Blomb. *in* Th. Fr. in *Bot. Notiser*: 155 (1867). *Leptorhaphis pithyophila* (Th. Fr. & Blomb.) Magnusson in *Förteckn. Skandinaviensis Växter* **4**: 10 (1936). *Pseudosagedia pithyophila* (Th. Fr. & Blomb.) Makarevicz, *in* Kopaczevskaja et al., *Opredelitel' lishainikov SSSR* **4**: 164 (1977). Type: Sweden, Närken, Götlunda, Hamrarna, on *Picea*, 1863, 1867, *O. G. Blomberg* (LD!—holotype).

Fig. 23B, 24.

Thallus: Greyish-brown, smooth, matt, continuous and not surrounded by a prothallus; superficial and immersed in the bark, composed of colourless, thin-walled, smooth and cylindrical hyphae, not constricted at the septa, less than 2 μm diam, difficult to observe; associated with trentepohlioid algae.

Ascomata: Blackish, shiny, smooth, numerous, scattered singly, circular to ellipsoidal, 200–250 μm diam; immersed in the bark, becoming superficial, hemispherical, mammiform, dimidiate; ostiole centrally located. Involucrellum: dark brown, *c.* 20–25 μm thick; consisting of a clypeate tissue composed of bark material intermixed with dark brown, thin- walled, smooth hyphae, *c.* 4 μm thick, constricted at the septa, forming a textura intricata, becoming a pseudoparenchymatous tissue of leptodermatous cells towards the ostiole; on occasions with crystalline inclusions at both sides of the ascomata. Exciple: not clearly differentiated. Hamathecium: of pseudoparaphyses, *c.* 2.5 μm wide; hymenial gelatin yellowish-amber in iodine. Asci: scanty, cylindrical-ovate, short-stalked, 60–85 × 23–26 μm; with two functional wall layers, the outer thin and smooth, the inner thicker towards the apex, with a pointed internal apical beak, not changing colour in iodine; 8-spored. Ascospores: biseriately arranged, colourless, smooth, with a thick epispore, narrowly ovate, (17.5–) 20–25 (–30) × 5.5–8 μm, 1-, 3-septate, constricted at the septa, especially the median septum, with enlarged middle cells and rounded apices, the lower cells slightly narrower than the upper; without differentiated gelatinous perispore.

Conidiomata: Not observed.

ECOLOGY. On smooth bark of *Pinus* and *Picea* branches and *Rhamnus frangula* L. [i.e. *Frangula alnus* Miller], together with other lichens, not causing any apparent damage; apparently lichenized with trentepohlioid algae.

DISTRIBUTION. Sweden, Götland, collected on several occasions in the type locality on three different hosts. Makarevicz (*in* Kopaczevskaja et al., 1977: 165) mentioned the species from Byelorussia and ASSR.

TYPIFICATION. Only one packet containing a mixed collection from 1863 and 1867 was located at LD, and this is here accepted as holotype since it fits the protologue.

OBSERVATIONS. *Arthopyrenia cerasi* (Schrader) Massal., a

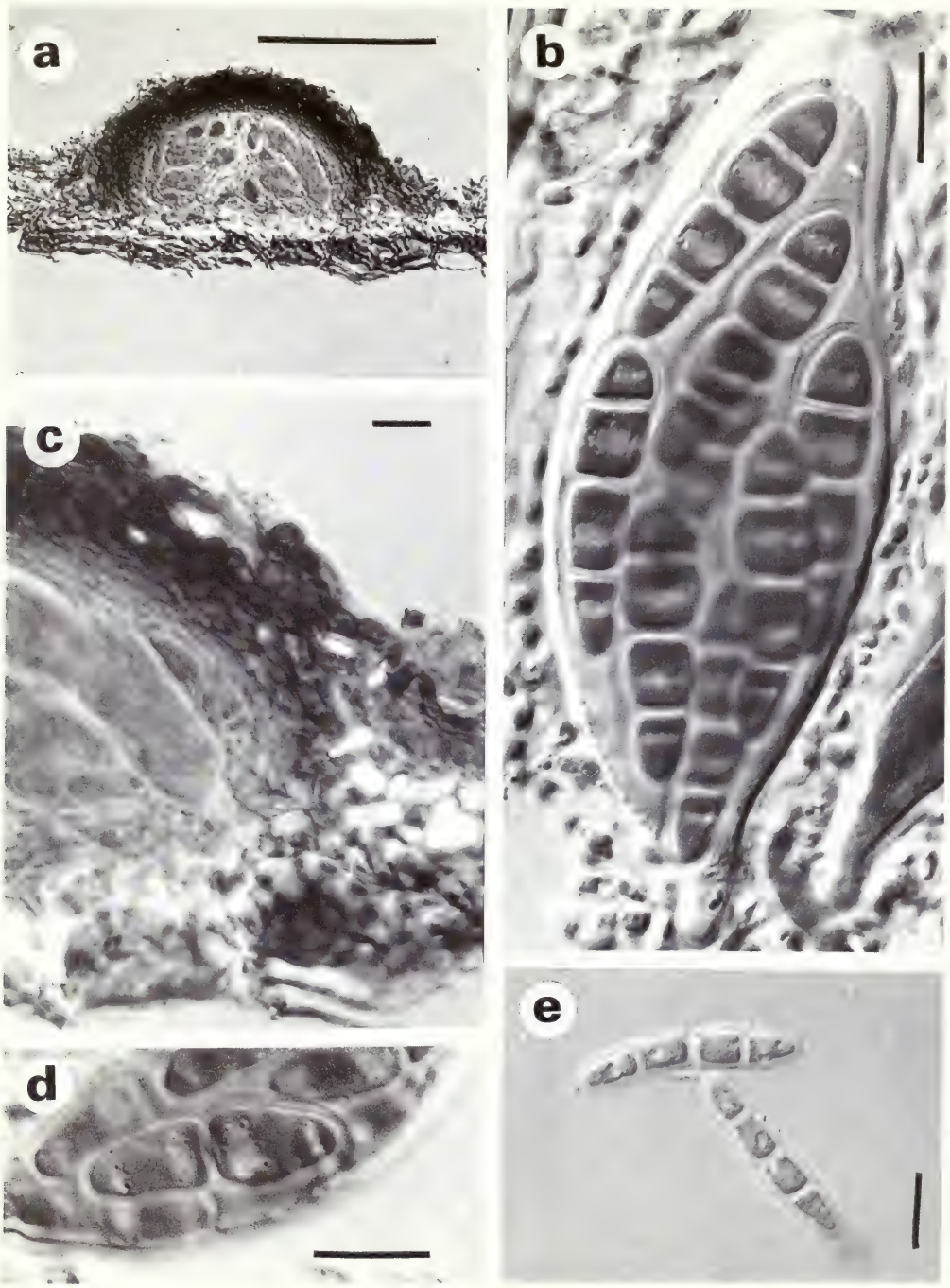


Fig. 24 *Arthopyrenia pithyophila* Th. Fr. & Blomb. (LD–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Involucrellum showing pseudoparenchymatous tissue of leptodermatous cells; (c) Pseudoparaphyses, ascus and ascospores; (d) Young ascospore; (e) Mature ascospores; scale = 10 μm.

species included in Harris' (1975) studies of the North American taxa, and which also occurs in Europe on smooth bark, may be closely related to *A. pithyophila*, on the basis of spore size and morphology and thallus characteristics, but the latter lacks a differentiated perispore, and the hamathecial tissues in *A. cerasi* are slender.

ADDITIONAL SPECIMENS. **Sweden**, Närken, Götlunda, Hamrarna, on *Picea*, 1868, *O. G. Blomberg* (UPS); loc. cit., on *Picea*, 1869, *O. G. Blomberg* (LD-3 specimens; PC-HUE 3491/4); loc. cit., on bark of *Pinus* sp., 1869, *O. G. Blomberg* (LD); loc. cit., on *Rhamnus frangula*, 1877, *O. G. Blomberg* (LD); loc. cit., on *Rhamnus frangula*, 1880, *O. G. Blomberg* (LD-2 specimens; PC-HUE 3491/3); loc. cit., on *Rhamnus frangula*, 1883, *O. G. Blomberg* (LD, UPS).

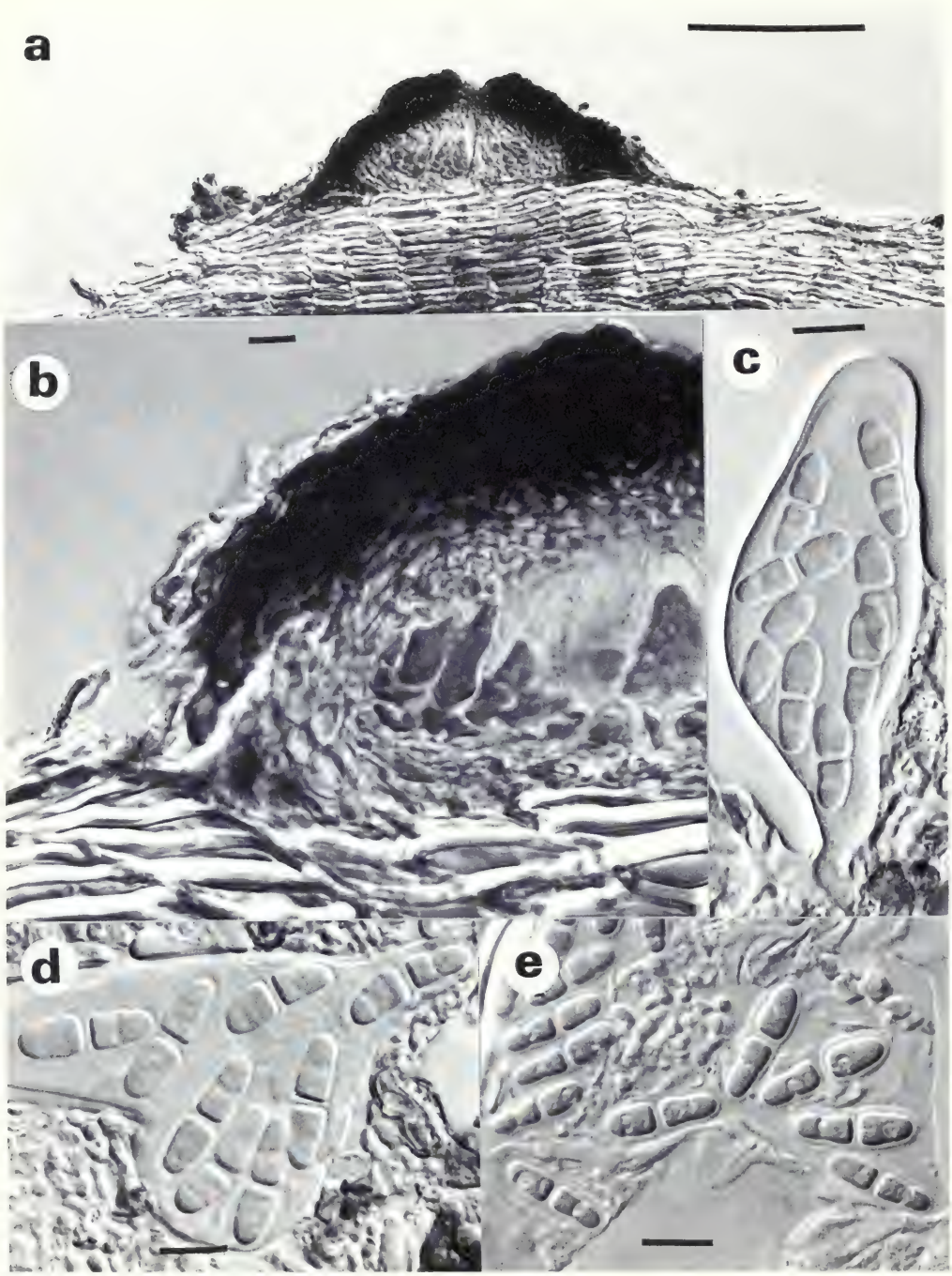


Fig. 25 *Arthopyrenia stenospora* Körber (L–syntype) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of involucrellum and exciple showing pseudoparenchymatic tissue of leptodermatous cells; (c) Ascus and ascospores; (d), (e) Ascospores; scale = 10 μm.

3. **Arthopyrenia stenospora** Körber, *Parerg. lich.*: 390 (1865). *Leptorhaphis stenospora* (Körber) Magnusson in *Förteckn. Skandinaviens Växter* **4**: 11 (1936). Type: Switzerland, Zürich, 'auf der Rinde junger Stänien von *Acer pseudoplatanus*' [Hepp, *Flech. Eur. exs.* no. 454, as *Pyrenula punctiformis* var. *acerina*] (L!–syntype).

Fig. 25, 26A.

Thallus: Inconspicuous, having the same colour as the bark; composed of colourless to dark brown, thin-walled, smooth and cylindrical hyphae, *c.* 2 μm diam, constricted at the septa, sometimes associated with trentepohlioid algae.

Ascomata: Dark brown to black, shiny, smooth, numerous, scattered singly, circular, 100–250 μm diam; immersed in the bark, becoming superficial, hemispherical, *c.* 60 μm in height, dimidiate; ostiole centrally located. Involucrellum: dark brown, 14.5–20 μm thick; consisting of a clypeate tissue, composed of bark material intermixed with dark brown, thin-walled and

smooth hyphae, forming in places a pseudoparenchymatic tissue of isodiametric cells, *c.* 3–4.5 µm, with an enlarged lumen and dark brown walls. Exciple: colourless, intergrading with the involucrellum; composed of colourless, thin-walled, isodiametric cells with enlarged lumina, forming a pseudoparenchymatous tissue of textura angularis. Hamathecium: of pseudoparaphyses, *c.* 2.5 µm broad; hymenial gelatin amber in iodine. Asci: scanty, ripening sequentially, cylindrical-ovate, ventricose, short-stalked, 60–70 × 23–27 µm; with two functional wall layers, the outer thin and smooth, the inner thicker towards the apex, with a small pointed internal apical beak, not changing colour in iodine; 8-spored. Ascospores: irregularly arranged in the asci, colourless, epispore thick and smooth, narrowly ovate, 15–23 × 4–6.5 µm, 1-septate, slightly constricted at the septa, usually somewhat unequal, with a narrower lower cell, which sometimes is also slightly constricted without becoming septate, perispore occasionally swelling in water and KOH.

Conidiomata: Not observed.

ECOLOGY. On smooth bark of *Acer pseudoplatanus* L., *Quercus robur* L., *Alnus glutinosa* (L.) Gaertner, and other trees, associated with other *Arthopyrenia* species and other lichens, not causing any apparent damage; loosely associated with trentepohlioid algae, but probably not lichenized.

DISTRIBUTION. Widely distributed in Scandinavia and central Europe; perhaps widespread in temperate regions. Makarevicz (in Kopaczevskaja et al., 1977) also described the species from USSR.

TYPIFICATION. When Körber (1865: 390) described this taxon, he based his description on the morphological characteristics of two different exsiccates: Zwackh *Lich. exs.* no. 108, as *Verrucaria punctiformis* Pers., and Hepp *Flecht. Eur. exs.* no. 454, as *Pyrenula punctiformis* var. *acerina* Hepp. He could not find ascospores in Hepp's exsiccate, but on the basis of Hepp's ascospore drawings assumed that both taxa were related. Only Hepp's material was located at L. Unfortunately this material contains two different *Arthopyrenia* species, ascospore sizes of which do not correspond with one another: one with ascomata *c.* 300–500 µm diam and ascospores 25–30 × 6–7 µm, and the second species described above with ascomata *c.* 100–250 µm diam, and ascospores 15–23 × 4–6.5 µm. One more collection of Hepp's exsiccate was located at K, and studied. This specimen has applanate ascomata, *c.* 300–500 µm and ascospore size 17–23 × 6–7 µm, similar to that in Hepp's description. Since type material from Zwackh *Lich. exs.* no. 108 was not studied, and Hepp's material only corresponded in ascospore size and morphology, the species concept accepted here is based on the material with smaller ascomata and ascospores located at L. However this should not been taken as a lectotypification, and the application of the name still remains uncertain until Zwackh's exsiccate material, studied by Körber, is located.

OBSERVATIONS. The specimen here described as *Arthopyrenia stenospora* seems taxonomically related to the broad species concept of *Arthopyrenia punctiformis*, which Harris (1975: 61) believed to include two different species: *A. padi* Rabenh. and *A. salicis* Massal. The former differs from *A. salicis* in its persistent hamathecial tissue and longer and narrower ascopores, which resemble those of *A. stenospora* together with other ascoma and ascospore characteristics, such as their shape and the presence of a thin perispore. Nevertheless, the taxon here described is included separately, until the species concepts in *A. punctiformis s. lat.* and *A. padi*, and some other taxa (e.g. *A. laburni* Arnold and *A. cembrina* (Anzi) Gaummann ex D. Hawksw.) are definitively clarified (Coppins, 1988: 310).

ADDITIONAL SPECIMENS. **Austria**, Tyrol, Trini, am Tramerbushe, August 1876, *B. Stein* (WRSL). **Norway**, Troms, 'in insula Lenjerd ad Skaterk', 30 June 1879, *J. M. Norman* (O). Vestfold, Larvik, Tvelane, 19 May 1882, *J. M. Norman* (O). Soslresenden, Holmestrand, Nyreian, *J. M. Norman* (O). Trøndelag, Lùmdems paroch., Stóren, on *Alnus*, *J. M. Norman* (O). Nordland, Storaarend paroch., Tysfjorden, 5 August 1878, *J. M. Norman* (O). **Poland**, Zielona Góra, 'Grünberg', Hellerig (WRSL); loc. cit., 'an Eichen', *V. Everken* (WRSL). 'Holting', August 1878, *B. Stein* (WRSL). **Sweden**, Orebro, 'Orebyo', *Th. Fries* (WRSL). **Switzerland**, Zürich, on bark of young *Acer pseudoplatanus*, April 1877, *G. Winter* (WRSL).

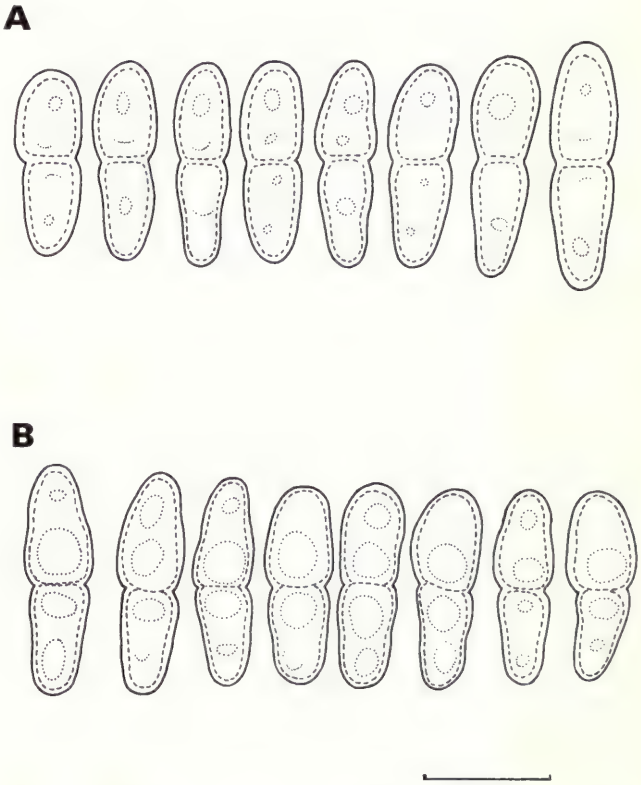


Fig. 26 Ascospore outlines (A) *Arthopyrenia stenospora* Körber (L–syntype); (B) *Arthopyrenia umbripicta* Norman (O–holotype); scale = 10 µm.

4. **Arthopyrenia umbripicta** Norman in *Ofvers. K. VetenskAkad. Förh. Stockh.* **41**(8): 38 (1885) ['1884']. *Leptorhaphis umbripicta* (Norman) Magnusson in *Förteckn. Skandinaviens Växter* **4**: 11 (1936). Type: Norway, Vetsfold, Holmestrand, Järnbaneparken, on *Fraxinus*, *J. M. Norman* (O!—holotype; UPS!—isotype).

Fig. 26B, 27.

Thallus: Olivaceous-brown, nearly black around the ascomata, smooth, matt, continuous, not delimited by a prothallus; superficial and immersed in the bark, superficially composed of dark brown, thin-walled, smooth hyphae, *c.* 4 µm

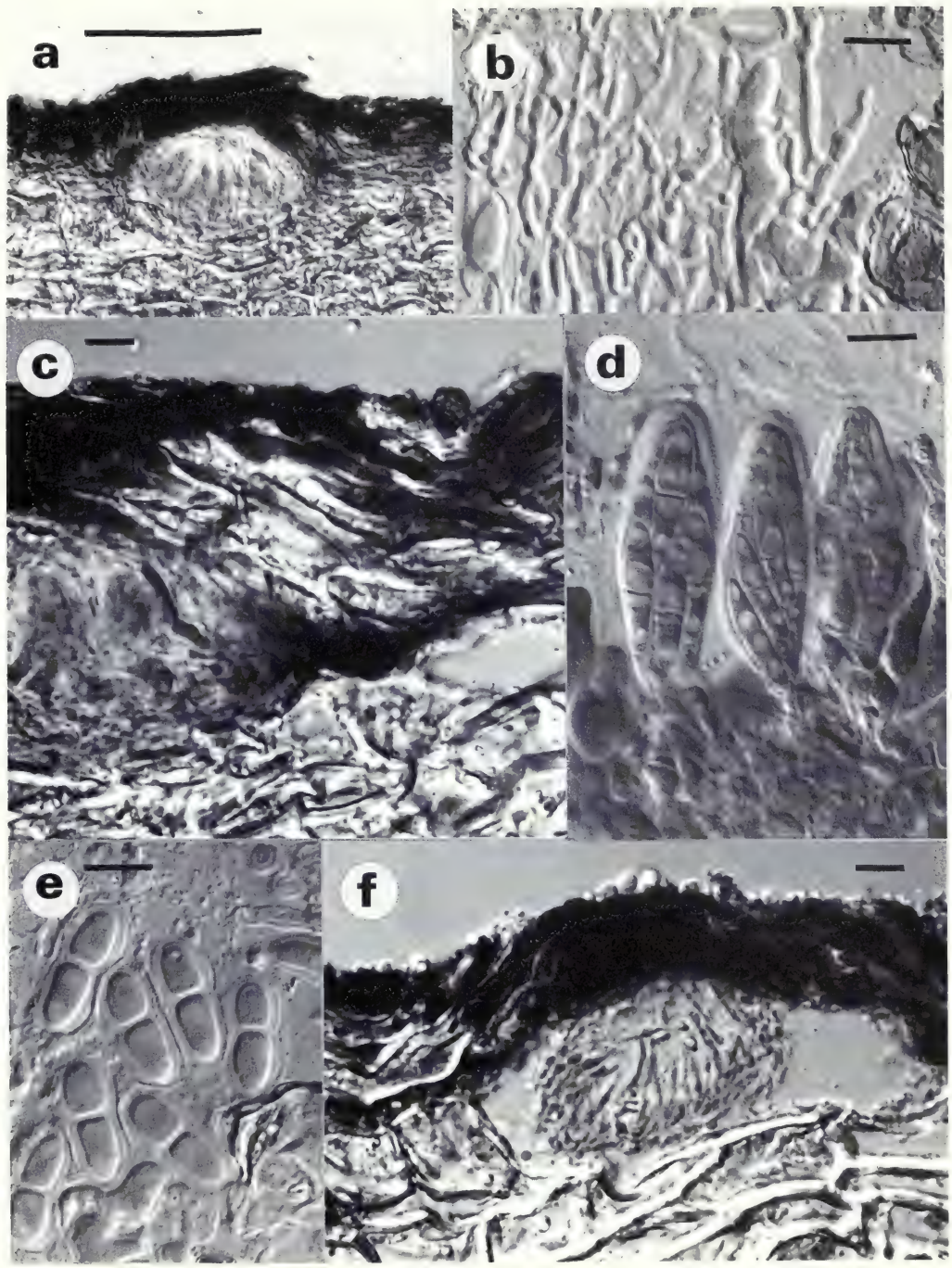


Fig. 27 *Arthopyrenia umbripicta* Norman (O–holotype). (a) Vertical section of ascoma; scale = 100 μm; (b) Pseudoparaphyses; (c) Detail of involucrellum showing clypeus; (d) Asci and ascospores; (e) Ascospores'; (f) Conidioma and conidia; scale = 10 μm.

wide, more or less moniliform, constricted at the septa, becoming colourless and thinner when immersed; not associated with algal cells.

Ascomata: Blackish, shiny, smooth, numerous, scattered singly, circular, 100–180 μm diam; almost completely immersed in the substratum, only a small area becoming superficial, hemispherical, *c.* 70 μm in height, dimidiate; ostiole centrally located. Involucrellum: dark brown, *c.* 15 μm thick, consisting of a clypeus, composed of bark material intermixed with dark brown nearly black, thick-walled, smooth hyphae, *c.* 4 μm thick, constricted at the septum, sometimes moniliform, forming a textura intricata, becoming epidermoidea in places. Exciple: colourless, intergrading with the involucrellum, composed of colourless, thin-walled isodiametric cells, with small lumen, forming a pseudoparenchymatous tissue of textura angularis. Hamathecium: of pseudoparaphyses, *c.* 2.5 μm wide; hymenial gelatin not changing colour in iodine. Asci: scanty, cylindrical- ovate, ventricose,

short-stalked, 35–45 × 15–17 µm, with two functional wall layers, the outer thin and smooth, the inner becoming thicker at the apex, with a short pointed internal apical beak, not reacting with iodine; 8-spored. Ascospores: irregularly arranged in the asci, colourless, with a thick and smooth epispore, narrowly ovate, 17–20 × 3.5–5.5 µm, 1- septate, constricted at the septum, with somewhat unequal cells, the lower narrower and smaller, with rounded apices, without a differentiated perispore.

Conidiomata: Pycnidial, blackish, shiny, smooth, scattered singly, circular, *c.* 100 µm diam; immersed in the substratum, globose; ostiole centrally located. Wall: dark brown, *c.* 20 µm thick; consisting of a clypeus composed of bark material intermixed with dark brown, nearly black, thin-walled, smooth hyphae, constricted at the septum forming in places a pseudoparenchymatous tissue of isodiametric cells, *c.* 4 µm wide, with dark brown walls and enlarged lumen. Conidiogenous cells: colourless, thin-walled, lageniform, *c.* 6 µm in length, arising from smaller, colourless, isodiametric cells directly adjacent to the wall. Conidiogenesis: apparently enteroblastic. Microconidia: colourless, aseptate, thin-walled, smooth and bacilliform, 7–10 × 1 µm.

ECOLOGY. On smooth bark of *Fraxinus excelsior* L. with another species of *Arthopyrenia*, forming patches and not causing apparent damage; apparently not lichenized.

DISTRIBUTION. Europe, Scandinavia, Norway, only known from the type locality.

TYPIFICATION. Two type collections were located at O and UPS. Material from O is here regarded as the holotype, since Norman's herbarium is known to be kept there (Hawksworth, 1974; Holmgren et al., 1981), the remaining collection from UPS being an isotype.

OBSERVATIONS. Only the type material of this species, growing on *Fraxinus* bark, from O and UPS has been located and studied. An additional specimen under this name from O, on *Tilia*, collected at the same locality, represents a different *Arthopyrenia* species, with smaller asci and ascospores, but with a similar dark olivaceous brown thallus. The latter was previously identified by Keissler as *Arthopyrenia cinerescens*, but it is perhaps a misidentification and I prefer not to apply the name. Indeed, *A. umbripicta* is only tentatively accepted here as a distinct *Arthopyrenia* species, and might prove to be synonymous with some other European taxon included in the genus and not discussed by Harris (1973, 1975).

III. **Celothelium** Massal.

Celothelium Massal. in *Atti Ist. veneto Sci. III*, **5**: 332 (1860). *Tomasellia* sect. *Celothelium* (Massal.) Müll. Arg. in *Bot. Jb.* **6**: 398 (1885). Type species: *Verrucaria socialis* Zenk. [*Celothelium socialis* (Zenk.) Massal.] (holotype).

Thallus: Smooth, greyish-white, crustose, very thin, slightly shiny, continuous, sometimes surrounded by a dark prothallus; endophloeodal, composed of colourless to pale brown, thin-walled, smooth and cylindrical hyphae, sometimes constricted at the septa; associated with trentepohlioid algae, and mixed with bark cells.

Ascomata: Perithecioid, black and brittle, shiny, smooth, numerous, individual to confluent, circular to ellipsoidal, sometimes elongated, and then reminiscent of lirellae; immersed in the substratum, becoming superficial, hemispherical, dimidiate and applanate, with several non-periphysate ostioles, in a central or marginal small papilla. Involucrellum: covering individual or groups of ascomata, composed of irregularly radiating reddish-brown, thick-walled hyphae, not changing colour in KOH, intermixed with bark cells, forming a clypeate tissue of textura epidermoidea to intricata; not extending beyond the ascomata in a basal fringe. Exciple: same colour as the involucrellum and intergrading with it, sometimes not extending below the ascomata. Hamathecium: of paraphysoids, composed of colourless, smooth, anastomosing, narrow, thin-walled hyphae, with infrequent septa, not constricted at the septa, forming a net surrounded with mucus; hymenial gelatin amber to bluish-green in iodine, but never deep blue. Asci: ripening sequentially probably from a crozier system, arising from the base or angles of the ascomatal cavity, narrowly elongated and cylindrical, short-stalked; two functional wall layers observed, the outer layer thin and smooth, the inner thickening at the top, sometimes showing a small internal apical beak, generally capped by a meniscus apparent in Congo red; 8-spored; discharge presumably fissitunicate. Ascospores: arranged in a fascicle, sometimes helically twisted, colourless, thin-walled, smooth, very long and filiform, multiseptate, not constricted at the septa, each cell containing numerous refringent particles, attenuated at the apices, without appendages or gelatinous sheaths.

Conidiomata: When present, pycnidial or stromatic, circular to elongated, black, shiny, smooth, scattered singly, numerous; immersed in the bark, becoming superficial, globose; ostiole centrally or marginally located. Wall: dark brown to black, covering and surrounding the conidioma, composed of bark material mixed with dark brown, thin-walled and smooth hyphae, forming a clypeus of textura epidermoidea to intricata; on the base, composed of hyaline to pale brown hyphae, mixed with bark material. Conidiogenous cells: colourless, thin-walled, more or less lageniform, arising from colourless and isodiametric cells, adjacent to the surrounding wall, sometimes marginally located. Conidiogenesis: presumably enteroblastic. Macroconidia: colourless, filiform, thin-walled, smooth, multiseptate, each cell containing numerous refringent particles. Microconidia: not observed.

NUMBER OF SPECIES. In the present account seven species have been recognized in the genus, most of which appear to be lichenized. These species occur in both temperate and tropical zones, and it is likely that additional species will be discovered, especially in the tropics where a greater part of the lichen and fungal flora still remains poorly known, and others have been omitted as a result of being included in other disparate genera, such as *Melanotheca* Fée, which have not been the subject of any modern revisions. At least three more taxa referred to *Melanotheca* sect. *Celothelium* are now in study, and it is likely that they belong to *Celothelium*. The species within the genus are distinguished primarily by the appearance of the ascomata, presence of a distinct exciple, ascus and ascospore size, and iodine reaction.

ECOLOGY. On smooth bark of deciduous trees and shrubs. The species appear to be lichenized with a trentepohlioid photobiont.

DISTRIBUTION. Europe and tropical Central and South America and Asia.

TYPFICATION AND NOMENCLATURE. The genus *Celothelium* Massal. (1860: 332) has been regarded as synonymous with

Melanotheca Fée (Hawksworth et al., 1983: 70; Eriksson & Hawksworth, 1987*a*: 23), a genus typified by *Trypethelium anomalum* Ach. [*Melanotheca anomala* (Ach.) Massal.] according to Farr et al. (1979: 1063). Other authors, such as Keissler (1938: 430) following Müller Argoviensis (1885: 398), referred to the genus as a section of *Tomasellia* Massal. Nevertheless *Celothelium* was described by Massalongo as having acicular ascospores, which somewhat resemble those of *Campylacia* [i.e. *Leptorhaphis* Körber], and also he designated *Verrucaria socialis* Zenk. as its type. This species described by Zenker (*in* Goebel & Kunze, 1829) from Guyana on 'guanaco' bark, was at the time and later mistaken for *Verrucaria aggregata* Fée [*Melanotheca aggregata* (Fée) Müll. Arg.], both species having similar coloured thalli, and showing certain resemblence in the ascomata clusters. The study of different isotypes of *Verrucaria socialis* Zenk. from Guyana collected by Cl. Leprieur and kept at PC (721-lectotype, selected here; 635, 1241, 1253-isolectotypes) showed that the taxon should be excluded from the genus *Melanotheca* Fée, differing from *M. aggregata* (Fée) Müll.Arg. in ascospore morphology.

A second generic name *Celothelium* has been attributed to Trevisan in 1860 (Hawksworth et al., 1983; Eriksson & Hawksworth, 1987*b*). However, Trevisan only published *Conspectus Verrucarinarum* in this year, where no mention of such a generic name can be found, and his *Synopsis generum Trypetheliarum* where he described the genus *Coenoicia*, selecting *Trypethelium nudum* Fée [i.e. *Coenoicia nuda* (Fée) Trev.] as a typical example of the genus (Trevisan, 1861: 22), with oblong to ellipsoidal ascospores, was not published until a year later. Pages below (1861: 25), in some additional annotations, *Celothelium* Massal. is referred to as being synonymous with *Coenoicia* and having priority over it: '*Celothelium* ist ganz und gar dieselbe Gattung wie meine *Coenoicia*; Massalongo's Name hat aber die Prioriät'. Two species were then included by Trevisan in Massalongo's genus: *Celothelium nudum* (Fée) Trev. and *C. leprieurii* Trev., the latter differing from the former in its acicular ascospores. However, I believe that both genera should be kept apart, and perhaps *Celothelium leprieurii* Trev. will prove to be the same species as *C. socialis* (Zenk) Massal., since the material studied by Trevisan was also from Guyana. Recently, Harris (1989: 82) listed *Coenoicia* as a synonym of *Pyrenula*, being the type of the genus *C. nuda* morphologically very close to *Pyrenula anomala* (Ach.) Vainio.

Relationships. At present the genus cannot be placed in a completely satisfactory systematic position since detailed studies on the ontogeny of these fungi have not been carried out. The presence of a differentiated pseudostroma in some of the species, paraphysoids and the asci apical meniscus, however, suggest that it belongs to the Pyrenulales rather than Dothideales.

Traditionally the generic name *Celothelium*, as a synonym of *Melanotheca* or *Tomasellia*, has been included among the Trypetheliaceae (Müller Argoviensis, 1885; Keissler, 1938). More recently the genus *Tomasellia* Massal. has been considered congeneric with *Mycoporellum* and *Mycoporopsis*, on the basis of ascus morphology, and treated as a member of the Pleosporaceae (Müller & von Arx, 1962; Harris, 1975), or the Arthopyreniaceae Watson (Eriksson & Hawksworth, 1987*a*). The ascus apical structure and morphology in *Celothelium*, cylindrical with a short apical dome, sometimes capped by a meniscus, apparent in Congo red, recall the family Acrocordiaceae Oxner, but differ in the hamathecial ontogeny; for nomenclatural discussion and consideration of the systematic position of the Acrocordiaceae see Eriksson (1981).

Some members of the genus such as *C. cinchonarum* and *C. socialis* present similar types of ascomata structure as the Trypetheliaceae where individual or groups of ascomata immersed in a pseudostromata are covered by an involucrellum (Fig. 28a-b). In other species of the genus this is somewhat reduced to a clypeate and brittle involucrellum covering the ascomata, and the pseudostromata and exciple are intergrading with it and minimally present at the sides of the ascomata, or non-existent (Fig. 28c-d). Nevertheless the ascus apex is capped by a meniscus, not presenting the iodine negative ring reported by Eriksson (1981: 164) for the Trypetheliaceae.

The genus is tentatively referred to the order Pyrenulales, having characteristics perhaps intermediate between Acrocordiaceae and Trypetheliaceae like the ascus apex structure, hamathecial tissues and ascomata structure, although in *Celothelium* the ascospores lack the lenticular lumina characteristic of many members of the Pyrenulales.

Observations. Vainio (1915: 209) accepted the usage of *Celothelium* for two species, *C. aciculiferum* and *C. cinchonarum*, which he previously regarded as congeneric with *Leptorhaphis*. Nevertheless *C. dominicanum*, a species newly described, was placed in *Leptorhaphis* on the basis of lacking an algal layer. Consequently he regarded *Celothelium* as being lichenized, and *Leptorhaphis* as being an exclusively fungal genus.

A key to the species of *Celothelium* previously referred to *Leptorhaphis s. lat*, which includes *C. dominicanum*, is provided. *C. socialis*, type of the genus, is not included here, since it was not possible to measure the asci and the ascospores of the material at PC Cryptogamic Herbarium. Three other species: *Melanotheca agminella* Nyl. (1876) collected by C. Wright in Cuba, *Melanotheca simplicella* Nyl. (1864) collected by Crouan brothers in France, and *Tomasellia zollingeri* Müll. Arg. (1892) collected in Java and Mauritius, are now under study and are believed to be related to *Celothelium*. A forth species *Tomasellia himalayensis* Awasthi & M. Agarwal (1968) was described from Darjeeling District in India as 'to belong to the section *Celothelium* Müll. Arg. on account of its narrow, acicular and multiseptate spores'. The authors also noted that the iodine reaction of this taxon was 'persistently blue', unlike in *Celothelium*. Finally, in a recent account of the genus *Chiodecton* and allied genera, Thor (1990) listed *Tomasellia himalayensis* as synonym of *Chiodecton leptospermum* Müll. Arg.

Key to the species

1. Ascospores 50–80 (–85) × 1.5–2 µm 2
– Ascospores 80–110 × 1.5–3 µm 3

2(1). Thallus creamy white, surrounded by a prothallus; ostiole centrally located; exciple extending below the ascomata; conidiomata absent; West Indies ..... 4. **C. dominicanum**
– Thallus pale yellow, not surrounded by a prothallus; ostiole laterally located; exciple never extending below the ascomata; conidiomata present; USSR (Caucasus Mountains) ..... 2. **C. buxi**

3(1). Ascomata 0.3–0.5 mm diam, occasionally confluent; hymenial gelatin never bluish in iodine; ostiole centrally located; ascospores 90–100 × 2–3 µm; conidiomata stromatic; Asia (Sri Lanka) ..... 6. **C. stenobelum**

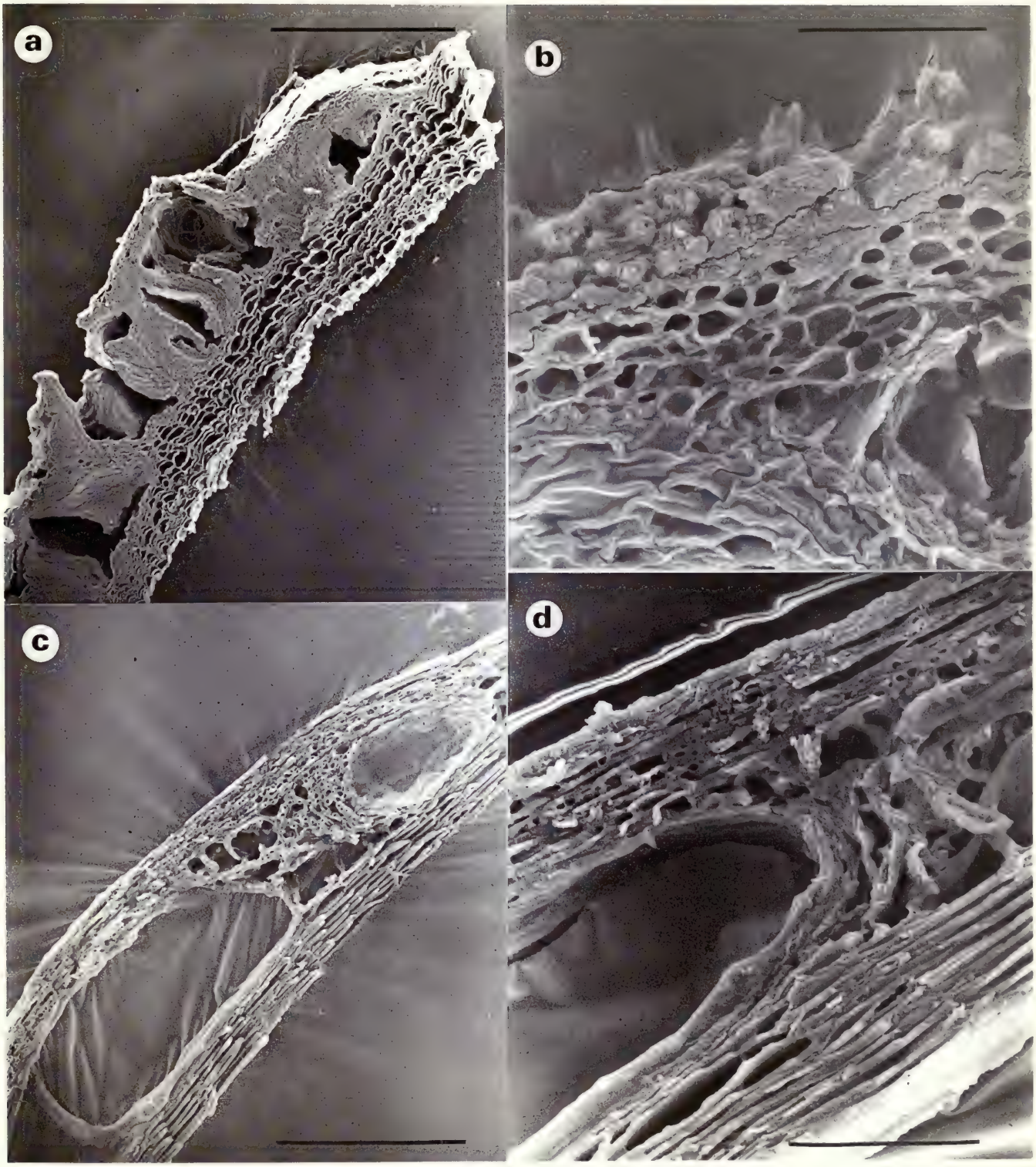


Fig. 28 *Celothelium cinchonarum* (Müll. Arg.) Vainio (G–holotype) (a) Vertical section of 'synascoma'; scale = 250 μm; (b) Detail of involucrellum and exciple showing textura angularis; scale = 27 μm. *Celothelium ischnobelum* (Nyl.) Aguirre (IMI 114732) (c) Vertical section of ascoma; scale = 86 μm; (d) Detail of involucrellum showing clypeus and exciple consisting of textura intricata; scale = 30 μm.

– Ascomata always exceeding 0.45 mm in diam; always confluent; hymenial gelatin bluish or not in iodine; ostiole centrally or laterally located; ascospores narrower: 80–110 × 1.5–2 μm; conidiomata pycnidial 4

4(3). Thallus whitish, not surrounded by a prothallus; ascomata 4.5–10 mm in length; ostiole centrally located; involucrellum hyphae dark brown; exciple well differentiated, extending below the ascomata; South America (Brazil) ..... 3. **C. cinchonarum**

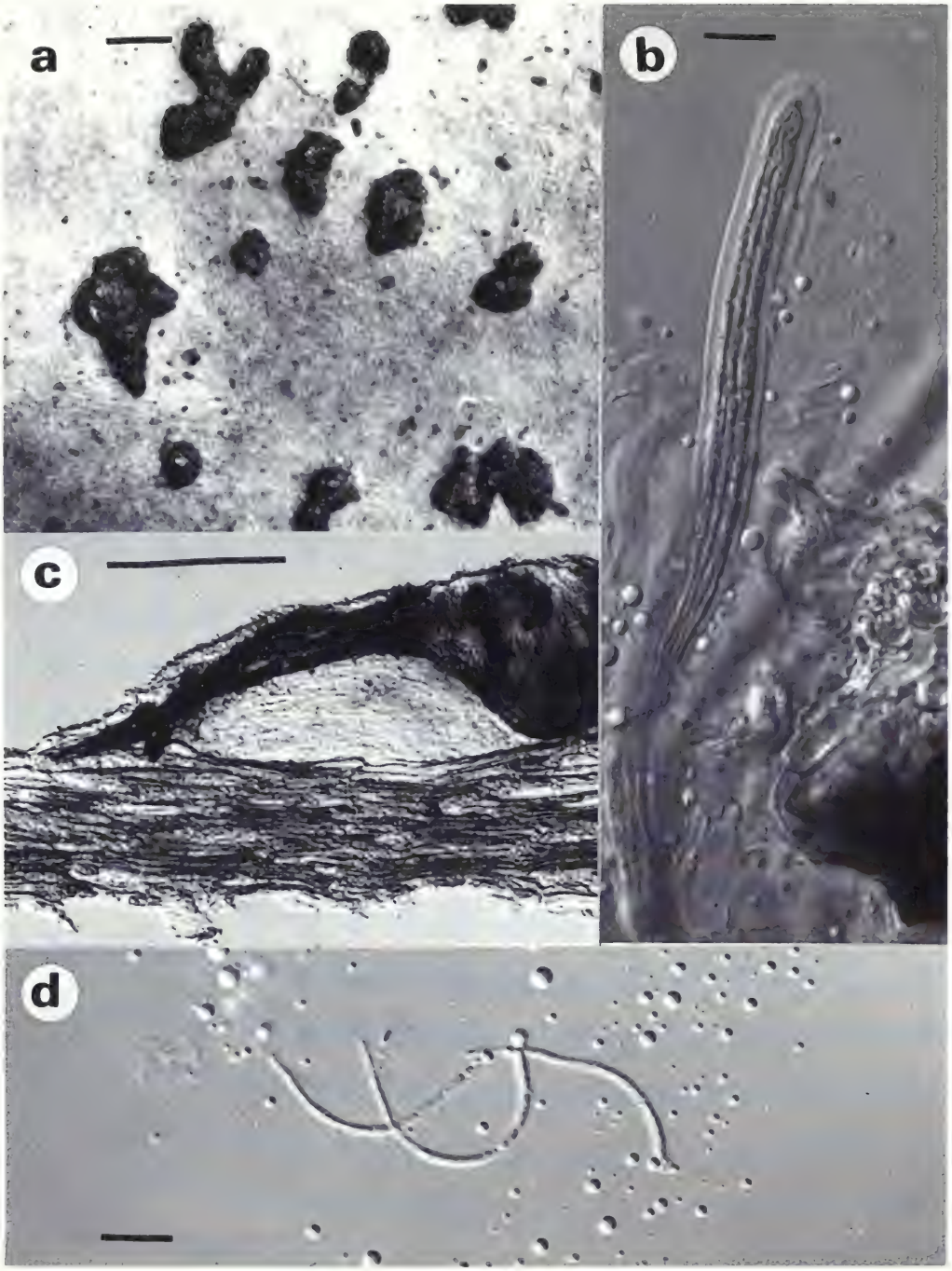


Fig. 29 *Celothelium aciculiferum* (Nyl.) Vainio (H–NYL 4303–isotype) (a) Surface view; scale = 500 μm; (b) Ascus and ascospores; scale = 10 μm; (c) Vertical section of ascoma; scale = 100 μm; (d) Ascospores; scale = 10 μm.

– Thallus never whitish, surrounded by a prothallus; ascomata 0.45–3 mm in length; ostiole laterally located; involucrellum hyphae reddish-brown; exciple not well differentiated 5

5(4). Thallus cream, pale yellow or greenish; hymenial gelatin bluish in iodine; ascus apex rounded; conidiomata pycnidial; western Europe ..... 5. **C. ischnobelum**

– Thallus silver-grey; hymenial gelatin never bluish in iodine; ascus apex slightly pointed; conidiomata absent; central and South America ..... 1. **C. aciculiferum**

The species

1. **Celothelium aciculiferum** (Nyl.) Vainio in *Suomal. Tiedeakat. Toim.* A. **6**(7): 209 (1915). *Melanotheca aciculifera* Nyl. in *Mém. Soc. hist. nat. sci. Cherbourg* **4**: 71 (1858). *Athrismidium aciculiferum* (Nyl.) Trev., *Consp. Verruc.*: 16 (1860). *Tomasellia aciculifera* (Nyl.) Müll. Arg. in *Bot. Jb.* **6**: 398 (1885). *Leptorhaphis aciculifera* (Nyl.) Vainio in *Acta Soc. Fauna Flora fenn.* **7**(2): 230

(1890). Type: French Guyana, 'ad corticem laevem (Mèlinon)' (PC!—holotype; H-NYL 4303!—isotype).

Melanotheca rhaphidiza Stirton in *J. Linn. Soc. Bot.*, **17**: 155 (1878); nom. inval. (Art. 32.1). Type: Honduras, Bahia Island, 'Lichens of the Challenger expedition' (BM!—holotype).

Fig. 29, 30.

Thallus: Smooth, silver-grey, slightly shiny, continuous and well delimited by an irregular black and narrow prothallus, less than 200 μm wide; immersed in the bark, composed of colourless, thin-walled, smooth, cylindrical hyphae, not constricted at the septa, less than 2 μm wide, difficult to observe, associated with trentepohlioid algae.

Ascomata: Perithecioid, black and brittle, shiny, smooth, numerous, generally confluent, forming a structure of irregular shape, more or less rounded, 1–3 mm diam, reminiscent of ascomata of the Arthoniales, circular to ellipsoidal when solitary, 140–260 μm diam; immersed in bark, becoming superficial, dimidiate, hemispherical, 70–150 μm high; ostiole in a marginal and small papilla, 40 μm wide. Involucrellum: dark brown, nearly black, brittle, covering and surrounding groups of ascomata except at their bases, 25–40 μm thick above each ascoma, up to 75 μm thick in the regions between ascomata; composed of bark material mixed with reddish- to dark brown, thick-walled hyphae, 2–4 μm wide, forming a textura epidermoidea in the external part of the wall, and grading to textura intricata on both sides of the ascoma towards the centrum. Hamathecium: of paraphysoids, less than 2 μm wide; hymenial gelatin amber in iodine. Asci: arising marginally, not numerous, cylindrical, short-stalked, 92–110 × 6.5–9.5 μm; two wall layers observed, the outer layer thin and smooth, the inner thickening at the apex, with a short internal apical beak; 8-spored. Ascospores: arranged in a fascicle in the ascus, sometimes twisted helically, colourless, thin-walled, smooth, filiform and 5-, 7 or 9-septate, *c.* 80 × 1.5–2 μm, attenuated at the apices.

Conidiomata: Not observed.

ECOLOGY. On unidentified smooth bark, growing with *Graphis elegans* (Borrer ex Sm.) Ach. and epiphytic bryophytes, not causing apparent damage; presumably lichenized with trentepohlioid photobiont.

DISTRIBUTION. Central and South America, in French Guyana (type locality), Colombia, Honduras and Brazil. Also known from two other localities in Brazil, Lafayette (1000m) and Carassa (1400m), according to Vainio (1890: 230).

TYPIFICATION. The material from Nylander's herbarium at PC is here regarded as the holotype, since reference to this particular specimen was included by Nylander in the original description. Consequently the second type collection located at H is regarded as isotype material.

Melanotheca rhaphidiza can be regarded as not validly published since Stirton (1878: 155) did not provide a species description, but it is also a superfluous name for *Celothelium aciculiferum* (Nyl.) Vainio. However, in the same article, Stirton referred to the species in a previous 'manuscript' which I have been unable to locate. Type material of *M. rhaphidiza* located in BM is here regarded as the holotype, and morphologically resembles *C. aciculiferum*.

OBSERVATIONS. When Trevisan (1860: 15) erected the genus *Athrismidium* for species with more or less ovoid and 3-septate ascospores, he included two taxa in the genus: *A. gelatinosum* (Chev.) Trevisan and *A. aciculiferum* (Nyl.) Trevisan, but presumably did not study authentic material of *Melanotheca aciculifera* Nyl. At present his genus is regarded as synonymous with *Tomasellia* (Eriksson & Hawksworth, 1987*a*), of which *T. gelatinosa* is the type species.

Celothelium aciculiferum differs from *C. cinchonarum* in forming more rounded patches when the perithecia are confluent, reminiscent of some Arthoniales; in the lack of a differentiated exciple and pseudostroma, and the presence of a prothallus. It also differs from *C. ischnobela* in the colour of the thallus, iodine reaction, bigger ascomata, and shorter ascospores.

ADDITIONAL SPECIMENS. **Brazil**, Minas Gerais, Sitio, 1885 [Vainio, *Lich. Brasiliensis exs.* no. 1090, as *Leptorhaphis aciculifera* (Nyl.) Vainio] (BM). **Colombia**, 'Nova Granata', 1869, *Lindig* 2642 (BM).

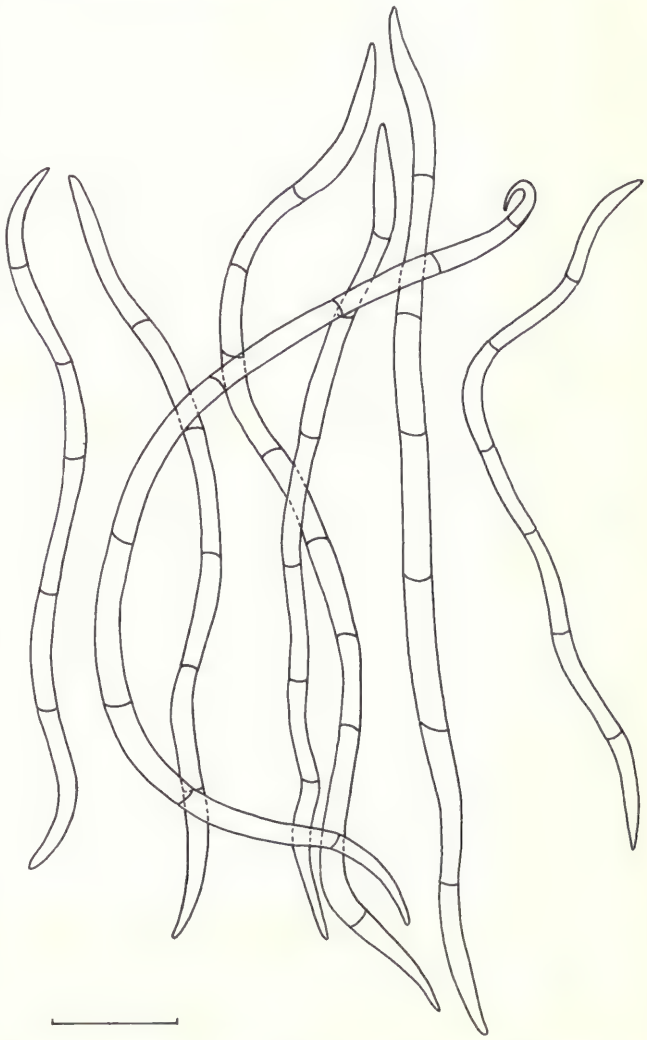


Fig. 30 Ascospore outlines of *Celothelium aciculiferum* (Nyl.) Vainio (H-NYL 4303–isotype); scale = 10 μm.

2. **Celothelium buxi** (Steiner) Aguirre, **comb. nov.**

Leptorhaphis buxi Steiner in *Annls mycol.* **17**: 4 (1919). Type: USSR, Caucasus Mountains, 'Tzebelda, Jurjewskoje', on bark of *Buxus sempervirens*, 4 June 1910, *G. Woronow* [*Lichenes Caucasi exs.* no. 226] (W 17954!—holotype).

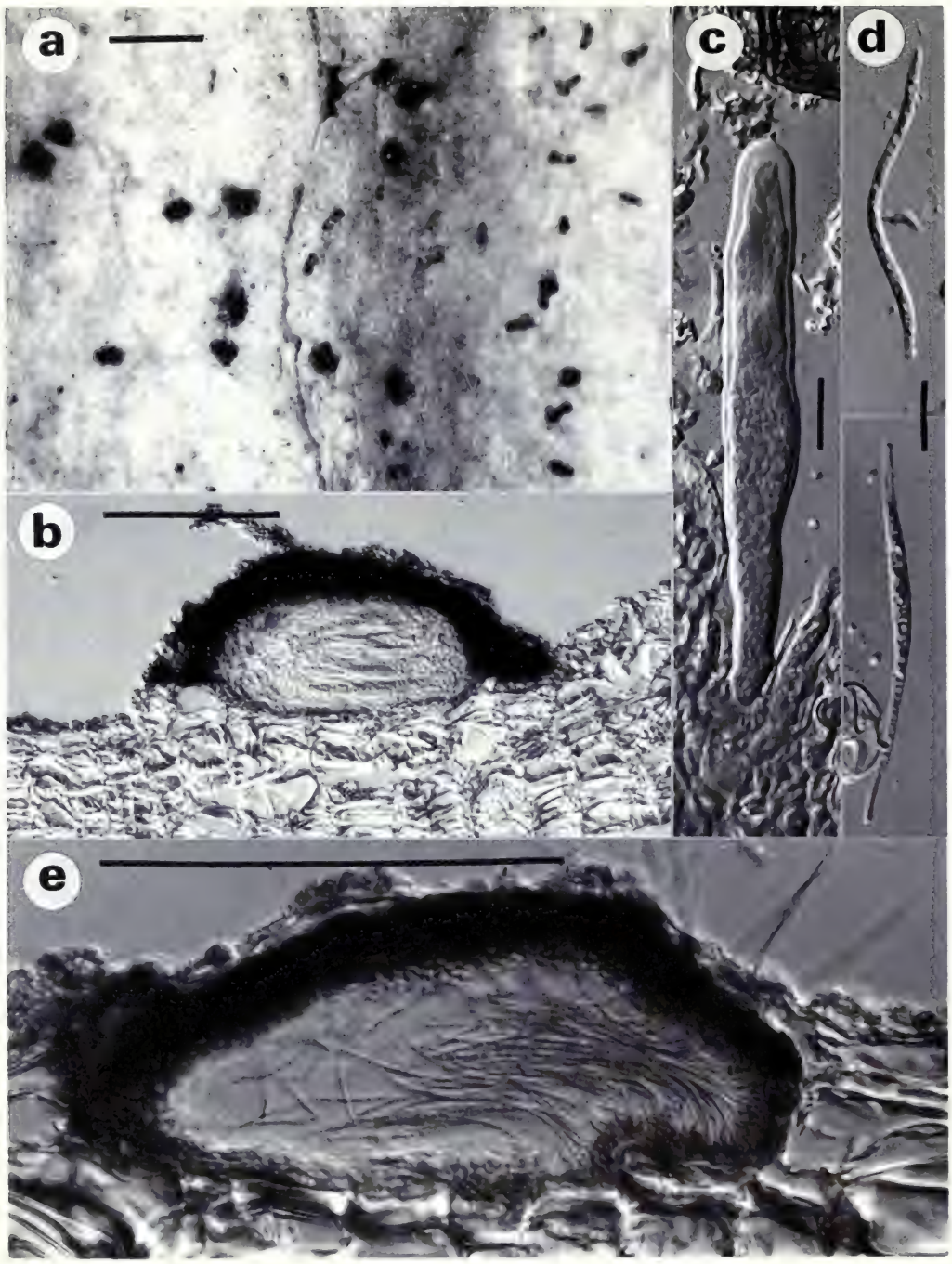


Fig. 31 *Celothelium buxi* (Steiner) Aguirre (W 17954–holotype) (a) Surface view of ascomata and conidiomata; scale = 500 μm; (b) Vertical section of ascoma showing marginal ostiole; scale = 100 μm; (c) Ascus and ascospores; (d) Ascospores; scale = 10 μm; (e) Conidioma and conidia; scale = 100 μm.

Fig. 31, 32.

Thallus: Smooth, pale yellow when dry, shiny, continuous, not surrounded by an apparent prothallus; superficial to immersed in the bark, composed of colourless to pale brown, thin-walled, smooth and cylindrical hyphae, not constricted at the septa and less than 2 μm wide, dichotomously branched; associated with trentepohlioid algae on the surface.

Ascomata: Perithecioid, black and brittle, shiny, smooth, scattered singly, circular to ellipsoidal, 200–300 μm diam; immersed in the bark, becoming superficial, hemispherical, dimidiate, with a marginal ostiole, *c.* 25 μm wide, not located in a papilla, placed near the surface of the bark. Involucrellum: dark brown, black in places, brittle, covering and surrounding the centrum except at its base, *c.* 25 μm thick; composed of bark material mixed with brown, thick-walled and smooth

hyphae, 2–3 µm diam, with darker walls, forming a textura intricata. Hamathecium: of paraphysoids, less than 2 µm wide; hymenial gelatin greenish in iodine. Asci: numerous, arising from the side of the ascoma opposite to the ostiole, cylindrical, short-stalked, 70–76 × 6–8.5 µm, ascus base *c.* 5.5–8 µm; two wall layers observed, the outer layer very thin and smooth, the inner thicker, the cytoplasmic contents narrowing near the apex forming an internal apical beak; 8-spored. Ascospores: arranged in a fascicle in the ascus, twisted helically, colourless, thin-walled, smooth, filiform, 50–85 × 1.5–2 µm, 10- or more septate, attenuated at the apices.

Conidiomata: Pycnidia, elongated, black, shiny, smooth, scattered singly, 125–150 µm in length, mixed with the ascomata but most abundant at the edge of the thallus; immersed in the bark, becoming superficial, hemispherical, dimidiate; ostiole not observed. *Wall*: dark brown to black, about 15 µm thick; composed of bark material mixed with dark brown, thin-walled and smooth hyphae, 2–4 µm wide, forming a textura epidermoidea becoming intricata in both sides of the conidioma; the base composed of few colourless to pale brown hyphae, also mixed with bark material. Conidiogenous cells: colourless, thin-walled, smooth, more or less lageniform, 4–6 × 2.5 µm, arising from colourless isodiametric cells adjacent to the conidiomatal wall, arising marginally in the conidioma. Conidiogenesis: not observed. Macroconidia: colourless, filiform, 50–85 × 1.5–2 µm, thin-walled, smooth and 7-, 9- or more septate, each cell containing numerous refringent particles.

ECOLOGY. According to packet annotation on smooth bark of *Buxus sempervirens* L.; presumably lichenized, with a trentepohlioid photobiont.

DISTRIBUTION. Europe, Caucasus Mountains; known only from type locality.

TYPIFICATION. Only one specimen was located at W, which is taken to be the holotype.

OBSERVATIONS. *Celothelium buxi* differs from *C. ischnobelum*, also found in Europe, in the smaller ascomata, asci, ascospores and conidiomata, as well as in the lack of a distinctive prothallus and bluish iodine reaction.

3. **Celothelium cinchonarum** (Müll. Arg.) Vainio in *Suomal. Tiedeakat. Toim.* A, **6**(7): 209 (1915). *Tomasellia cinchonarum* Müll. Arg. in *Flora, Jena* **68**: 12 (1885). *Leptorhaphis cinchonarum* (Müll. Arg.) Vainio in *Acta Soc. Fauna Flora fenn.* **7**(2): 231 (1890). Type: Brazil, Minas Gerais Province, 'prope Sitio', 1000 m, on *Cinchona* bark, Hampe hb (G!–holotype).

Fig. 28, 33, 34.

Thallus: Irregular, whitish, matt, continuous, not delimited by a prothallus; immersed in the substratum, composed of bark material and colourless, thin-walled, smooth, cylindrical hyphae, loosely associated with trentepohlioid algae.

Ascomata: Black and brittle, shiny, smooth, numerous, always confluent, forming an elongated structure of irregular shape reminiscent of lirellae of the Graphidales, 4.5–10 mm in length; immersed in the bark, becoming superficial, individual ascoma flaskshaped, 160–190 × 180–220 µm, with an ostiole located in a central papilla, *c.* 45 µm wide.

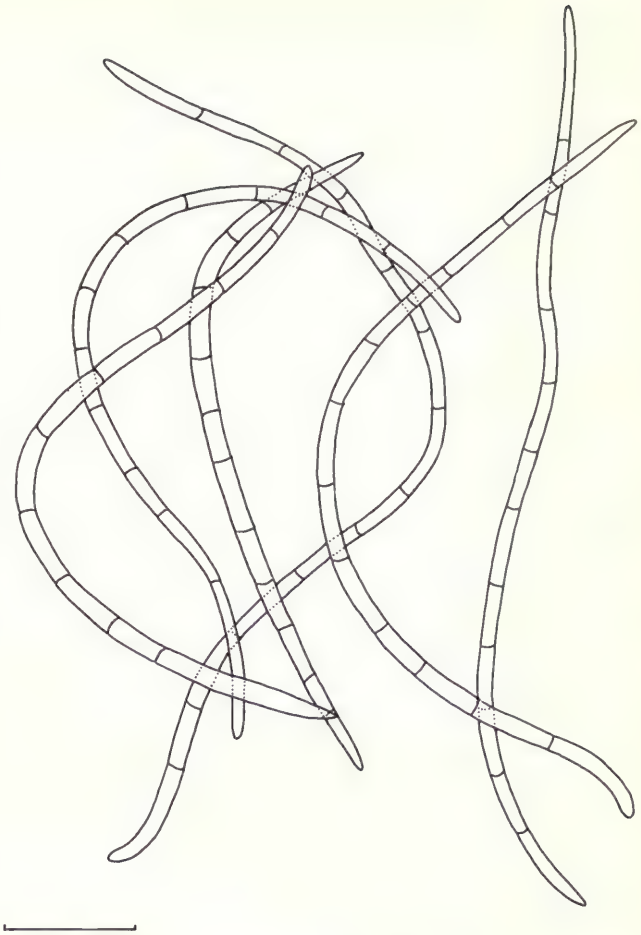


Fig. 32 Ascospore outlines of *Celothelium buxi* (Steiner) Aguirre (W 17954–holotype); scale = 10 µm.

Involucrellum: black, brittle, covering the ascomata, *c.* 45 µm thick; composed of bark material mixed with dark brown, thin-walled hyphae, *c.* 3 µm wide, forming a black tissue without recognizable textura. Exciple: intergrading with the involucrellum, surrounding the centrum, consisting of reddish brown hyphae intermixed with bark material forming a textura intricata. Hamathecium: of paraphysoids, less than 2 µm wide; hymenial gelatin not changing colour in iodine. Asci: numerous, arising from the base of the ascomata, cylindrical, short-stalked, 90–110 × 10–12 µm, ascus base *c.* 4 µm wide; two wall layers observed, the outer thin and smooth, the inner without an apparent internal apical beak, not changing colour in iodine, but with a meniscus staining dark blue in cotton-blue near the apex; 8-spored. Ascospores: arranged in a fascicle in the ascus, sometimes twisted helically, colourless, thin-walled, smooth, filiform, *c.* 90 × 1.5–2 µm, 10- or more septate, attenuated at the apices.

Conidiomata: Not observed.

ECOLOGY. On *Cinchona* bark, growing on the projections of the bark, not causing apparent damage; probably lichenized, associated with trentepohlioid algae.

DISTRIBUTION. South America, Brazil; known only from type locality. Material of this species described by Awasthi & Agarwal (1968: 1025) from Darjeeling District in India is probably not related to *Celothelium*, since the hamathecial

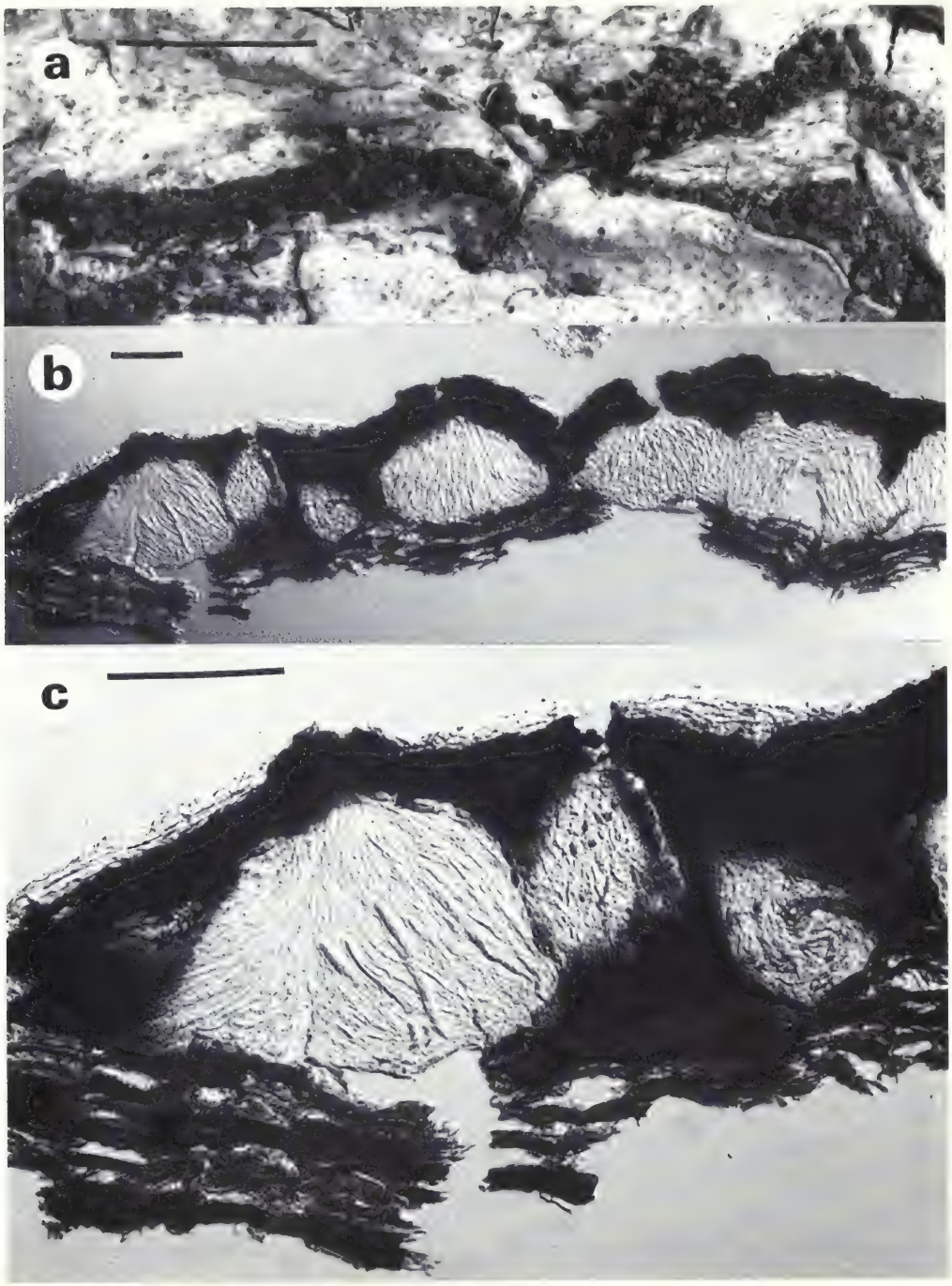


Fig. 33 *Celothelium cinchonarum* (Müll. Arg.) Vainio (G–holotype) (a) Surface view of ascomata; scale = 500 μm; (b), (c) Vertical section of ascomata showing pseudostroma; scale = 100 μm.

iodine reaction is reported as being deep blue becoming greenish-vinose (see p. 132)

TYPIFICATION. Only the holotype collection of this species is known.

OBSERVATIONS. This species differs from *Celothelium aciculiferum* in the colour of the thallus, the lack of a prothallus, and slightly bigger asci and ascospores.

The name *Glyphis repens* Meyer, which Zahlbruckner (1924: 487) included as synonymous with *Chiodecton hypoleucum* Nyl., was also handwritten on the packet. Nevertheless this material is not closely related to either the Graphidales or Opegraphales; this conclusion is based on my study of material of *Glyphis cicatricosa* Ach. [IMI 296207, 246141] and *Chiodecton perplexum* Nyl. [IMI 246091].

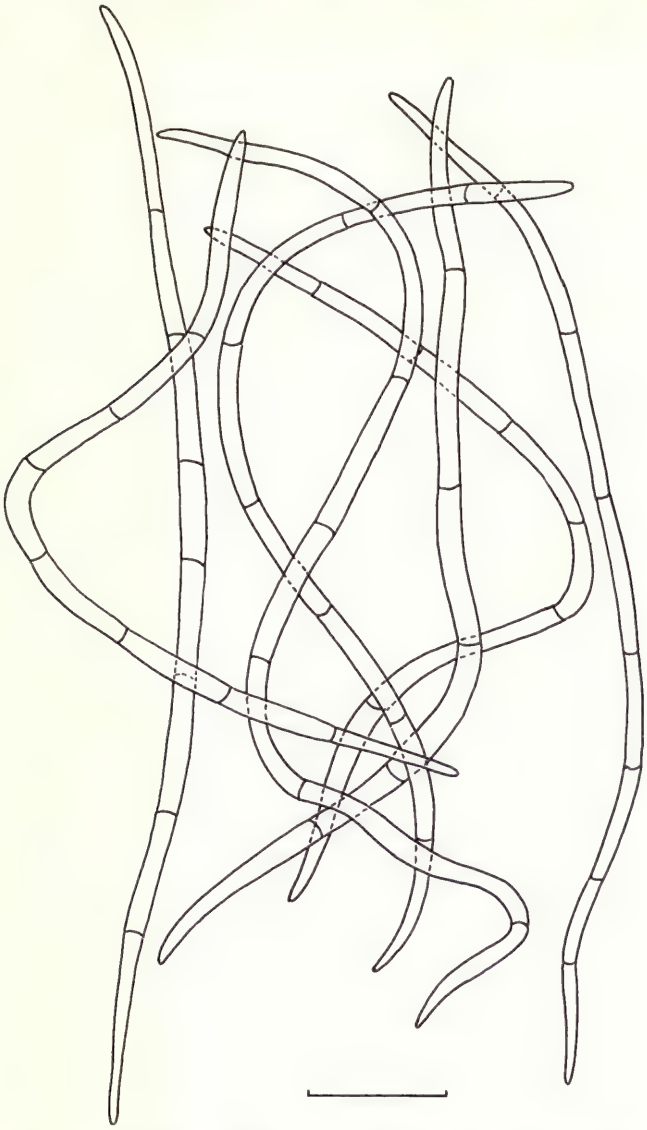


Fig. 34 Ascospore outlines of *Celothelium cinchonarum* (Müll. Arg.) Vainio (G–holotype); scale = 10 μm.

4. **Celothelium dominicanum** (Vainio) Aguirre, **comb. nov.**
Leptorhaphis dominicana Vainio in *Suomal. Tiedeakat. Toim.* A, **6**(7): 210 (1915). Type: West Indies, Guadeloupe, ['insula dominica'], Grande-Soufrière Mountain, 'ad corticem arbusti', 25 February 1896, *W. R. Elliott* (TUR 32697!—holotype).

Fig. 35, 36.

Thallus: Smooth, creamy-white, matt, continuous, delimited by an irregular, brown and narrow prothallus, less than 100 μm wide; immersed in the bark to a great depth, composed of colourless, thin- walled, smooth, cylindrical hyphae, less than 2 μm wide; apparently not associated with algae.

Ascomata: Black and brittle, shiny, smooth, scattered singly, sometimes confluent, circular to ellipsoidal, 200–400 μm diam; immersed in the bark, becoming superficial, hemispherical, dimidiate to complete when fully developed; ostiole, about 35 μm wide, located in a central papilla. Involucrellum: black, brittle, covering groups of two or three ascomata, *c.* 40 μm thick; composed of bark material mixed with dark brown, thick-walled hyphae, 2.5–4 μm wide, forming a clypeus of textura epidermoidea. Exciple: intergrading with the involucrellum, consisting of dark brown hyphae, intermixed with bark cells, forming a textura intricata. Hamathecium: of paraphysoids, less than 2 μm wide; hymenial gelatin not changing colour in iodine. Asci: not numerous, arising from the base of the ascoma opposite the papilla, cylindrical, short-stalked, 75–90 × 8.5–9.5 μm; two wall layers observed, the outer thin and smooth, the inner with a short internal apical beak; 8-spored. Ascospores: arranged in a fascicle in the ascus, sometimes twisted helically, colourless, thin-walled, smooth, filiform, *c.* 80 × 1.5–2 μm, attenuated at the apices, 7-, 9- or more septate.

Conidiomata: Not observed.

ECOLOGY. On smooth bark of unidentified shrubs, growing with *Didymosphaeria detincta* (Nyl. ex Müll. Arg.) Vainio [i.e. *Mycomicrothelia miculiformis* (Nyl. ex Müll. Arg.) D. Hawksw.]; apparently not lichenized.

DISTRIBUTION. America, West Indies; only known from type locality.

OBSERVATIONS. This species differs from *Celothelium buxi* in the colour of the thallus, the presence of a small prothallus and the inclusion of several ascomata under the same involucrellum, having a differentiated exciple. Both species have smaller ascomata, asci and ascospores than other members of the genus, *C. dominicana* having bigger asci than *C. buxi*. Vainio (1915: 210) excluded the species from *Celothelium* on the basis of the lack of a photobiont, referring the taxon to the genus *Leptorhaphis*, which he considered not lichenized. Nevertheless, characteristics such as the ascomatal and ascus structure, and ascospore morphology are closer to *Celothelium* than *Leptorhaphis*.

5. **Celothelium ischnobelum** (Nyl.) Aguirre, **comb. nov.**

Melanotheca ischnobela Nyl. in *Flora, Jena* **59**: 238 (1876). *Tomasellia ischnobela* (Nyl.) Keissler, *Rabenh. Krypt., Fl.* **9**, 1(2): 421 (1938). *Leptorhaphis ischnobela* (Nyl.) Coppins *in* Hawksworth et al. in *Lichenologist* **12**: 58 (1980). Type: British Isles, Eire, Co. Galway, Connemara Mountains, Kylemore Castle, 'ilicicola', February 1876, *Cl. du Bois Larbalestier* (BM!—lectotype, selected here; TCD!—isolectotype).

Verrucaria myriospora Leighton in *Trans. Linn. Soc. London* II, *Bot.* **1**: 145 (1876). Type: British Isles, Eire, Co. Galway, Kylemore Castle and Doughruagh Mountains, on young oaks, October 1875, *Cl. du Bois Larbalestier* (BM!—lectotype, selected here; BM!—isolectotype).

Leptorhaphis carrollii A. L. Smith in *J. Bot.* **49**: 42 (1911). Type: British Isles, Eire, Co. Cork, Glenbower Wood, 'ad corticem arborum', April 1869, *I. Carroll* (BM–type material lost)

Fig. 28, 37, 38.

Thallus: Smooth, greenish-white or pale yellow to creamish when dry, shiny, continuous, sometimes delimited by a dark brown prothallus, *c.* 300 μm wide; immersed in the bark, composed of colourless to pale brown, thin-walled, smooth and cylindrical hyphae, less than 4 μm wide, constricted at the septa, mixed with bark cells, associated with trentepohlioid algae below the surface.

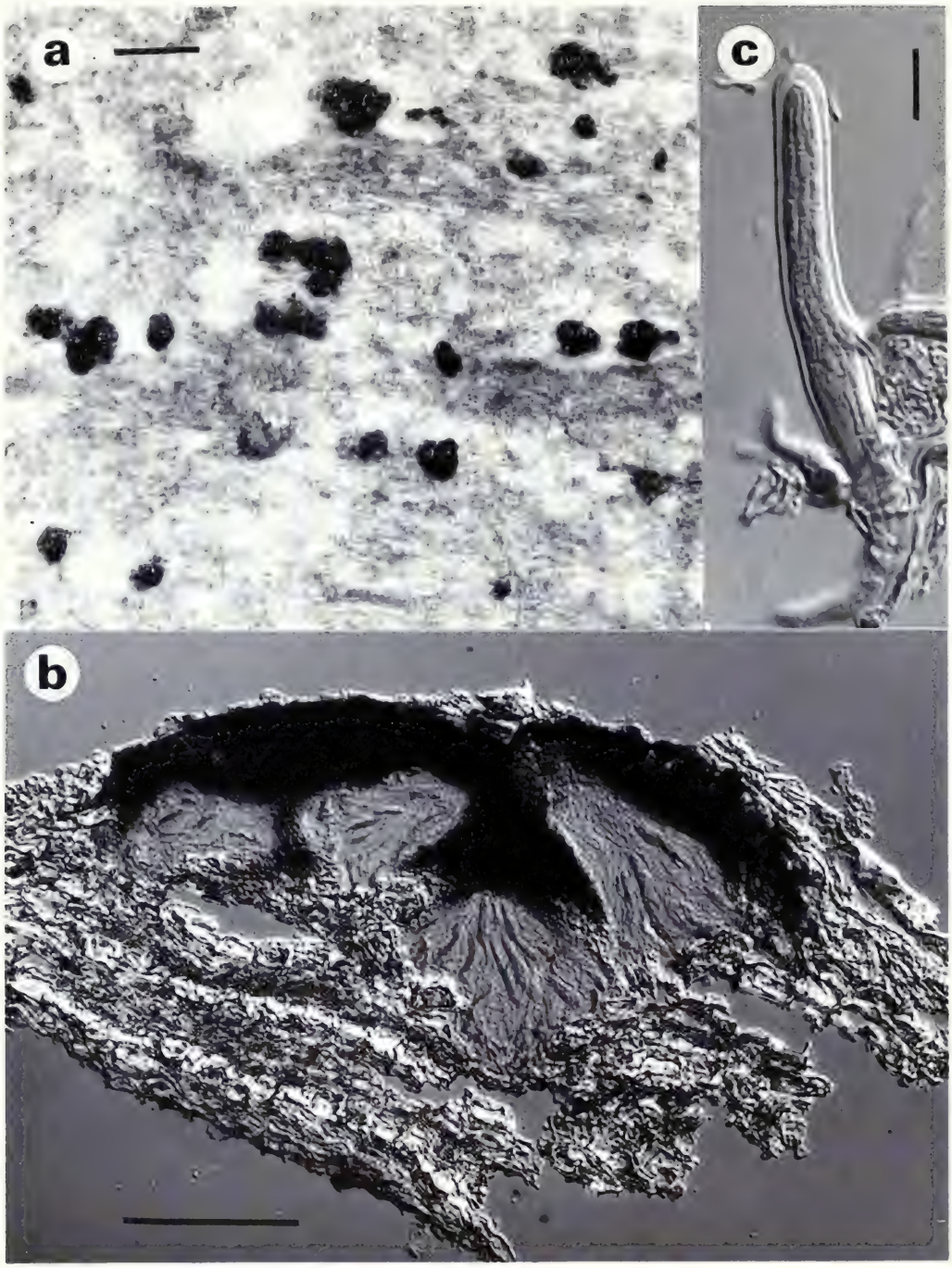


Fig. 35 *Celothelium dominicanum* (Vainio) Aguirre (TUR 32697–holotype) (a) Surface view of ascomata; scale = 500 μm; (b) Vertical section of ascomata; scale = 100 μm; (c) Ascus and ascospores; scale = 10 μm.

Ascomata: Black and brittle, shiny, smooth, scattered in groups of ascomata, circular to ellipsoidal, 0.45–1 mm diam; immersed in the substratum, becoming superficial, hemispherical to applanate, dimidiate, each ascoma 250–500 × 135 μm; ostiole located in a small central papilla. Involucrellum: blackish, brittle, covering groups of ascomata, *c.* 50 μm thick; composed of bark material mixed with reddish-brown thick-walled smooth hyphae, 2–3 μm wide, not changing colour with 10% KOH, forming a clypeus of textura epidermoidea. Exciple: intergrading with the involucrellum, mainly differentiated at the margins of the ascomata, sometimes extending below, colourless to brownish, *c.* 30–40 μm thick, sometimes thicker; consisting of colourless to brown hyphae intermixed with bark cells forming a textura intricata. Hamathecium: of paraphysoids, less than 2 μm wide; hymenial gelatin bluish in iodine. Asci: numerous, arising from the angles of the ascoma cavity, cylindrical, short-stalked, 80–110 × 6–10 μm; two wall layers observed, the outer layer thin and smooth, the inner

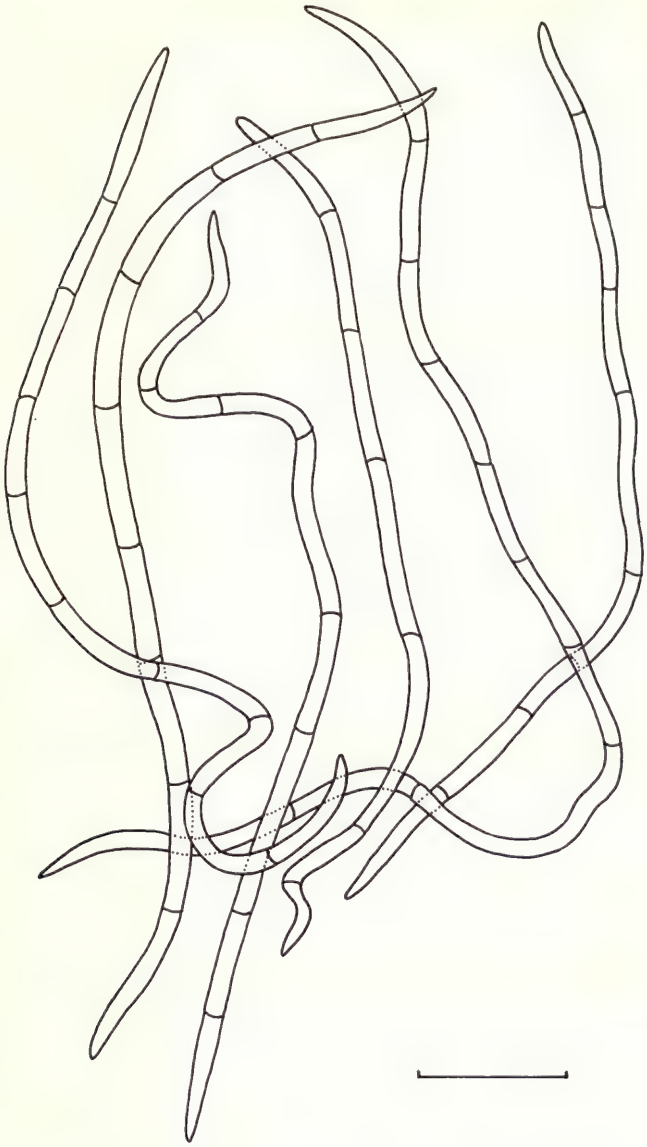


Fig. 36 Ascospore outlines of *Celothelium dominicanum* (Vainio) Aguirre (TUR 32697–holotype); scale = 10 μm.

without an apparent internal apical beak, not changing colour in iodine, but with a meniscus staining dark blue in cotton-blue near the apex and apparent in congo red; 8-spored. Ascospores: arranged in a fascicle, sometimes twisted helically, colourless, thin-walled, smooth, filiform, 80–110 × 1.5–2.5 μm, 8- or more septate.

Conidiomata: Pycnidial, circular to elongated, black, shiny, smooth, scattered singly, numerous, 400–600 μm in length; immersed in the bark, becoming superficial, hemispherical, dimidiate; ostiole not observed. Wall: dark brown to blackish, *c.* 20 μm thick; composed of bark material mixed with dark brown, thin-walled and smooth hyphae, 2–4 μm diam, constricted at the septa forming a textura epidermoidea, becoming intricata at both sides of the conidioma and towards the centrum; base of the conidioma formed by pale brown hyphae mixed with bark material. Conidiogenous cells: colourless, thin-walled, smooth, more or less lageniform, 7–10 × 1.5–2 μm, arising from colourless isodiametric cells located at base and angles of conidioma cavity. Conidiogenesis: presumably enteroblastic. Macroconidia: colourless, filiform, 60–100 × 1.5–2 μm, thin-walled, smooth and multiseptate, each cell containing numerous refringent particles.

ECOLOGY. On smooth bark of deciduous trees and shrubs, mainly on *Corylus avellana* L., in humid situations. Presumably lichenized, with trentepohlioid algae.

DISTRIBUTION. Known only from Europe. In the British Isles it has been collected from humid sites near the west and southern coast, and has a scattered distribution. A recent collection from Tuscany in Italy was studied, suggesting that it is present in other oceanic territories of Europe.

TYPIFICATION. Several syntypes and paratypes of both *Melanotheca ischnobela* Nyl. and *Verrucaria myriospora* Leighton have been studied from BM and TCD. These specimens were collected in Co. Galway (Eire) in two different localities: Connemara Mountains and Doughruagh Mountains. The material from the former locality on holly, and kept at BM, is here selected as a lectotype of *M. ischnobela*, since it seems to agree better with the protologue. For similar reasons and being the only material of *Verrucaria myriospora* collected on young oaks, one of the specimens at BM is here selected as a lectotype, and the remaining specimen as an isolectotype.

Material under the name of *Leptorhaphis carrollii* kept at BM now only bears *Mycomicrothelia confusa* D. Hawksw. and an *Arthopyrenia* species, probably *A. punctiformis s. lat.*. Additional original material was also searched for in Carroll's collections at E, DBN, and TCN, but not located. According to the description and illustrations provided by Smith (1911), the fungus had a very thin thallus, black perithecia, very thin and anastomosed 'paraphyses', and filiform ascospores, which were indistinctly multiseptate. This description and the ecology of the fungus satisfactorily agree with *Celothelium ischnobelum* as described here, and therefore both taxa are regarded as synonymous.

OBSERVATIONS. *C. ischnobelum* differs from the only other European taxon of the genus discussed here, *C. buxi*, in having wider ascomata, asci and ascospores. Swinscow (1965) described *C. ischnobelum* as having inconspicuous or non-existent thallus, and *Trentepohlia* is seen in fresh material. However, thin sections of dried herbarium material proved to have a thin fungal-algal layer below the surface; consequently I consider the species to be lichenized.

ADDITIONAL SELECTED SPECIMENS. **British Isles**, Eire, Co. Galway, Doughruagh Mountains, *c.* 600 m, on *Ilex aquifolium*, February 1876, *Cl. du Bois Larbalestier* (BM). Connemara Mountains, Kylemore Castle, on *Betula* sp. (BM). Kerry, Cromaglown, on hazel near stream, 28 June 1961, *T. D. V. Swinscow* (BM). Cork, Ballyrisode House, on holly in shade by road, 29 June 1961, *T. D. V. Swinscow* (BM). SW. Kenmore, Inchiquin Lough, Uragh woods, 15 August 1966, *P. W. James* (IMI 144732, 128432). England, Cumbria, Crosby Ravensworth, wood by stream to NE of Crosby Lodge, 210–245 m, on *Corylus* with *Bacidia vezdae*, 29 July 1979, *B. J. Coppins* 4272 (E). Hampshire, Andover, Caldridge Wood, on smooth bark of *Corylus*, April 1971, *B. J. Coppins & P. W. James* (BM). Waggoners Wells, locally abundant by stream in valley bottom, *on Corylus*, 23 October 1970, *B. J. Coppins & F. Rose* (BM, E). Wood Crates, W of Lyndhurst, by stream, on *Corylus*, 10 January 1973, *B. J. Coppins & F. Rose* (BM). Northumberland, wood by Wark Barn, W of

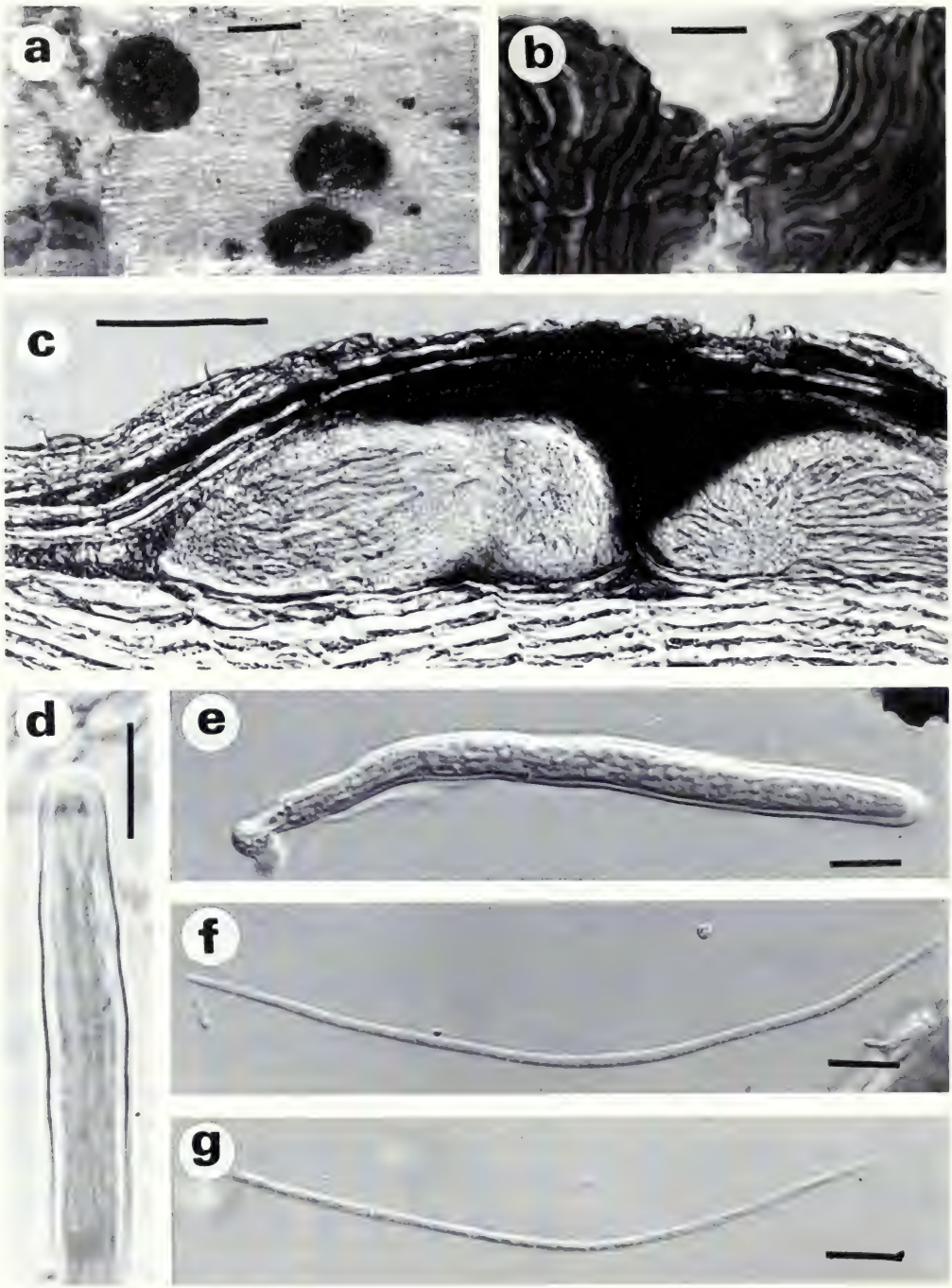


Fig. 37 *Celothelium ischnobelum* (Nyl.) Aguirre (BM–lectotype) (a) Surface view of ascomata; scale = 500 μm; (b) Detail of involucrellum (surface view); scale = 10 μm; (c) Vertical section of ascomata; scale = 100 μm; (d) Ascus apex capped by meniscus; (e) Ascus and ascospores; (f) Ascospore; (g) Conidia; scale = 10 μm.

Wark, on *Corylus* by stream, 18 May 1974, *B. J. Coppins* 375 (E). Somerset, Cleeve Combe, on *Corylus* and *Fraxinus*, 10 July 1934, *D. A. Jones* (BM). East Sussex, Hastings, Westfield, Maplehurst Wood, rare on *Corylus* by stream, 21 January 1973, *B. J. Coppins* (BM). West Sussex, Marden, North Marden Down, on *Corylus* in wood, 18 February 1971, *B. J. Coppins & F. Rose* (BM). Wiltshire, NW of Salisbury, Groveley Wood, on *Corylus*, in damp hollow in wood, 15 November 1972, *B. J. Coppins & F. Rose* (BM). Yorkshire, Midwest York, North of Wigglesworth, Hollow Gill Wood, 150 m, shaded *Corylus* with *Bacidia vezdae*, 17 October 1976, *B. J. Coppins* 2419 et al. (E). Northern Ireland, Co. Down, Ballynahinch, on hazel in dense shade of wood, 7 July 1961, *T. D. V. Swinscow* (BM). Scotland, Borders, Langstonlees Cleugh, 5 km SW of Duns, on *Corylus*, with *Bacidia vezdae*, 9 October 1981, *B. J. Coppins* PP21 (E). 'Central,

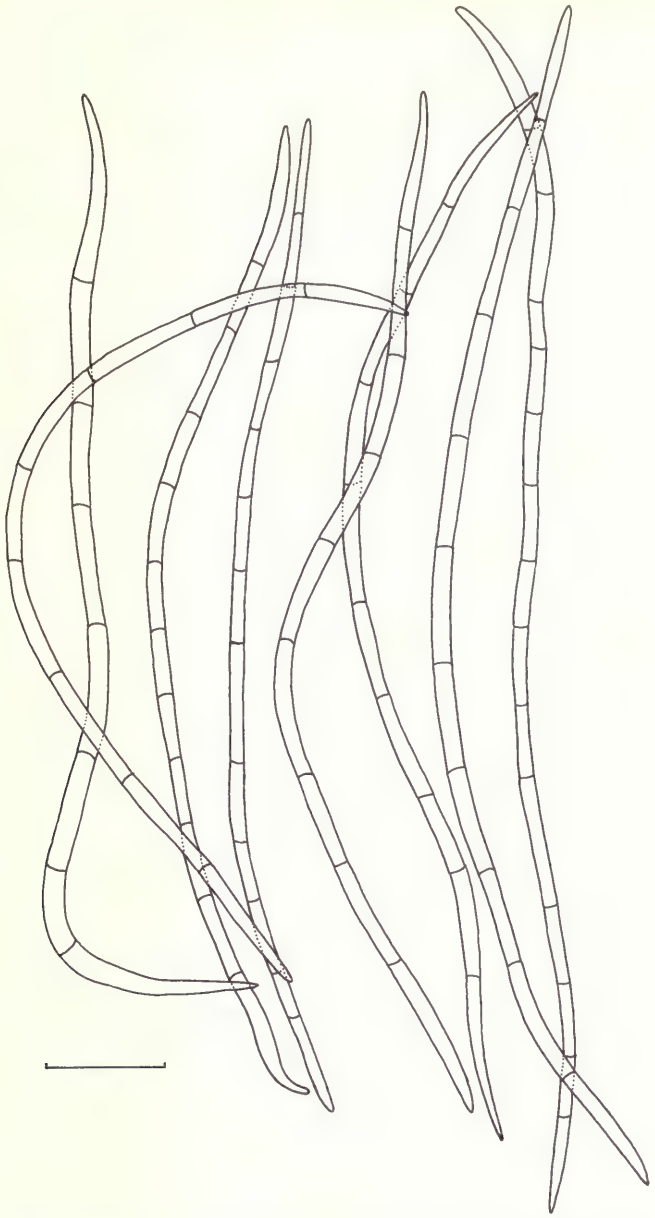


Fig. 38 Ascospore outlines of *Celothelium ischnobelum* (Nyl.) Aguirre (BM–lectotype); scale = 10 μm.

Clackmannan, Dollor Glen, near bottom of glen, rare on *Corylus*, 3 February 1974, *B. J. Coppins & P. B. Topham* 65 (E). Stirling, Inchcailloch, Loch Lomond, on *Corylus*, 17 May 1974, *B. J. Coppins* 349 (E). Hebrides, Mull, one mile east of Achronich, opposite Eorsa, in small gorge, on *Corylus*, 11 May 1968, *P. W. James* (BM). Highland, Westerness, N side of Loch Sunart, 1 km SE. of Salen, An Cnap, on *Corylus avellana* with *Thelotrema macrosporum*, 8 August 1983, *B. J. Coppins 9303 & P. M. Jørgensen* (E). Kintyre, Ellary Woods, by Obhaim Mnore, on *Corylus*, with *Micarea prasina* and *Arthonia tumidula*, 2 July 1976, *B. J. Coppins* 2626 (E). Strathclyde, Argyll, Seil Ballachuan, wood south of Pot Mor, on *Corylus*, 6 August 1980, *B. J. Coppins* 8112 (E). Tayside, W. of Perth, Kirkton Glen, Balguhidder Church, on *Corylus*, 1 April 1975, *B. J. Coppins* 765 (E). Middle Perth, Hermitage Glen, Dunkeld, on *Corylus*, 27 September 1975, *B. J. Coppins* 1137 (E). Wales, Gwynedd, Dolgellau, 1876, *W. A. Leighton* (BM). Powys, Brecon, New Port Melin-fâch, wood by Afon Nedd, 3 km NNE of Pont Nedd Fechan, on *Corylus*, 6 August 1984, *B. J. Coppins* 10933 & *R. G. Woods* (E). Dyfed, 13 km N of Llandovery, Allt Rhyd-y-groes, NNR wood SE of Cribyn Du, on *Corylus*, 24 July 1981, *B. J. Coppins* 8579 & *R. G. Woods* (E). **Italy**, Tuscany, Lucca prov., Alpi Apuane, Colli, side stream of Torrente Turrite Sicca, 600 m, small valley with *Corylus*, 30 April 1985, *B. J. Coppins, P. W. James & F. Rose* 12286 (E).

6. **Celothelium stenobelum** (Nyl.) Aguirre, **comb. nov.**

Verrucaria stenobela Nyl. in *Acta Soc. Scient. fenn.* **26**(10): 25 (1900). *Leptorhaphis stenobola* ['stenobela'] (Nyl.) Zahlbr., *Cat. lich. univ.* **1**: 344(1922). Type: Sri Lanka, Pidirutallegalle Mountain, 'corticola', 1879, *E. Almquist* (H-NYL 640!—holotype).

Fig. 39, 40, 41.

Thallus: Smooth, whitish-grey when dry, shiny, not continuous, not surrounded by a prothallus; superficial to immersed in the bark, composed of colourless to pale brown, thin-walled, smooth and cylindrical hyphae, constricted at the septa, less than 3 μm wide, dichotomously branched, associated with trentepohlioid algae on the surface.

Ascomata: Black and brittle, shiny, smooth, circular to ellipsoidal, sometimes surrounded by a dark fringe, scattered singly, 300–500 μm diam, occasionally confluent; immersed in the bark, becoming superficial, hemispherical, entire, ostiole centrally located. Involucrellum: dark brown, black in places, brittle, covering the ascomata, 60–70 μm thick; composed of bark material mixed with brown, thick-walled and smooth hyphae, 2–3 μm wide, with darker walls forming a clypeus of textura intricata. Exciple: dark brown, 20–40 μm thick, intergrading with the involucrellum, continuing at the base of the ascomata. Hamathecium: of paraphysoids, less than 2 μm wide; hymenial gelatin not changing colour in iodine. Asci: numerous, arising from the sides and base of the centrum, cylindrical, short-stalked, 80–100 × 9–10 μm, with a narrow hoof-like base, 4–6 μm wide; two wall layers observed, the outer wall thin and smooth, the inner without an apparent internal apical beak; 8-spored. Ascospores: arranged in a fascicle in the asci, sometimes twisted helically, colourless, thin-walled, smooth, filiform, 90–100 × 2–3 μm, attenuated at the apices, 9-, 11-or more septate.

Conidiomata: Stromatic, black, shiny, smooth, scattered singly, 150–200 μm diam; totally immersed in the bark, flask-shaped without a proper wall, opening to the surface through a neck about 100 μm wide, where the ostiole is located; composed of dark brown, smooth, thin- walled hyphae and bark material, forming a textura epidermoidea-intricata. Conidiogenous cells: colourless, thin-walled, smooth, more or less lageniform, 10–12 × 1.5 μm, each producing many conidia, arising from colourless cells adjacent to the surrounding bark material and hyphae. Macroconidia: colourless, filiform, curved, 18–25 × 1 μm, thin-walled, smooth and apparently not septate.

ECOLOGY. On bare and smooth unidentified bark, thallus

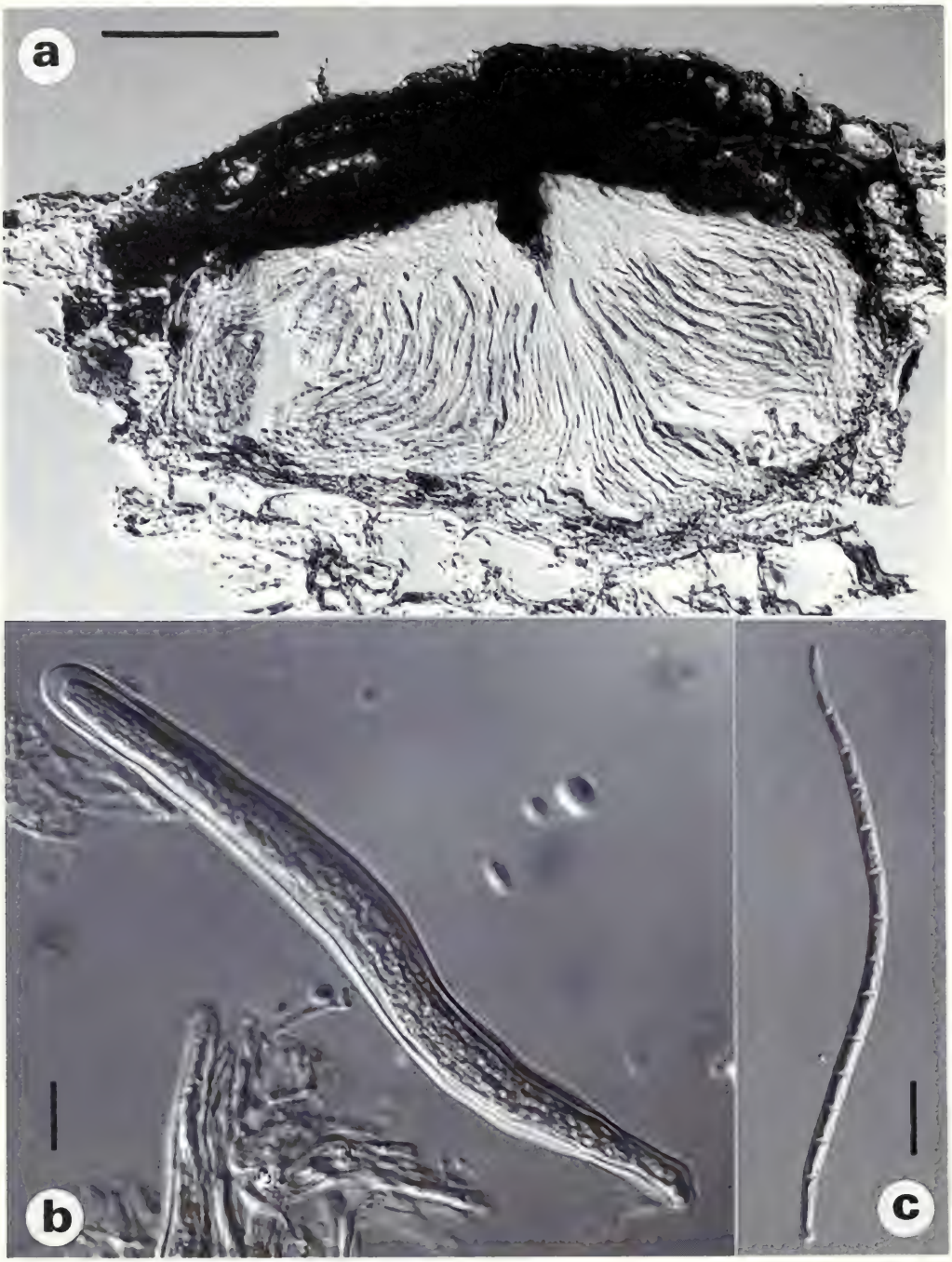


Fig. 39 *Celothelium stenobelum* (Nyl.) Aguirre (H-NYL 640–holotype) (a) Vertical section of ascoma; scale = 100 µm; (b) Ascus and ascospores; (c) Ascospore; scale = 10 µm.

discolouring the bark in places, but not causing any apparent damage; presumably lichenized with a trentepohlioid photobiont.

DISTRIBUTION. Sri Lanka, known only from the type locality.

TYPIFICATION. Only one type collection was located in Nylander's herbarium at H, which is here accepted as the holotype.

OBSERVATIONS. According to Zahlbruckner (1922: 344) the epithet *'stenobela'* is a typographic error and should be replaced by *'stenobola'*. Nevertheless the information written in the packet at Nylander's herbarium does not

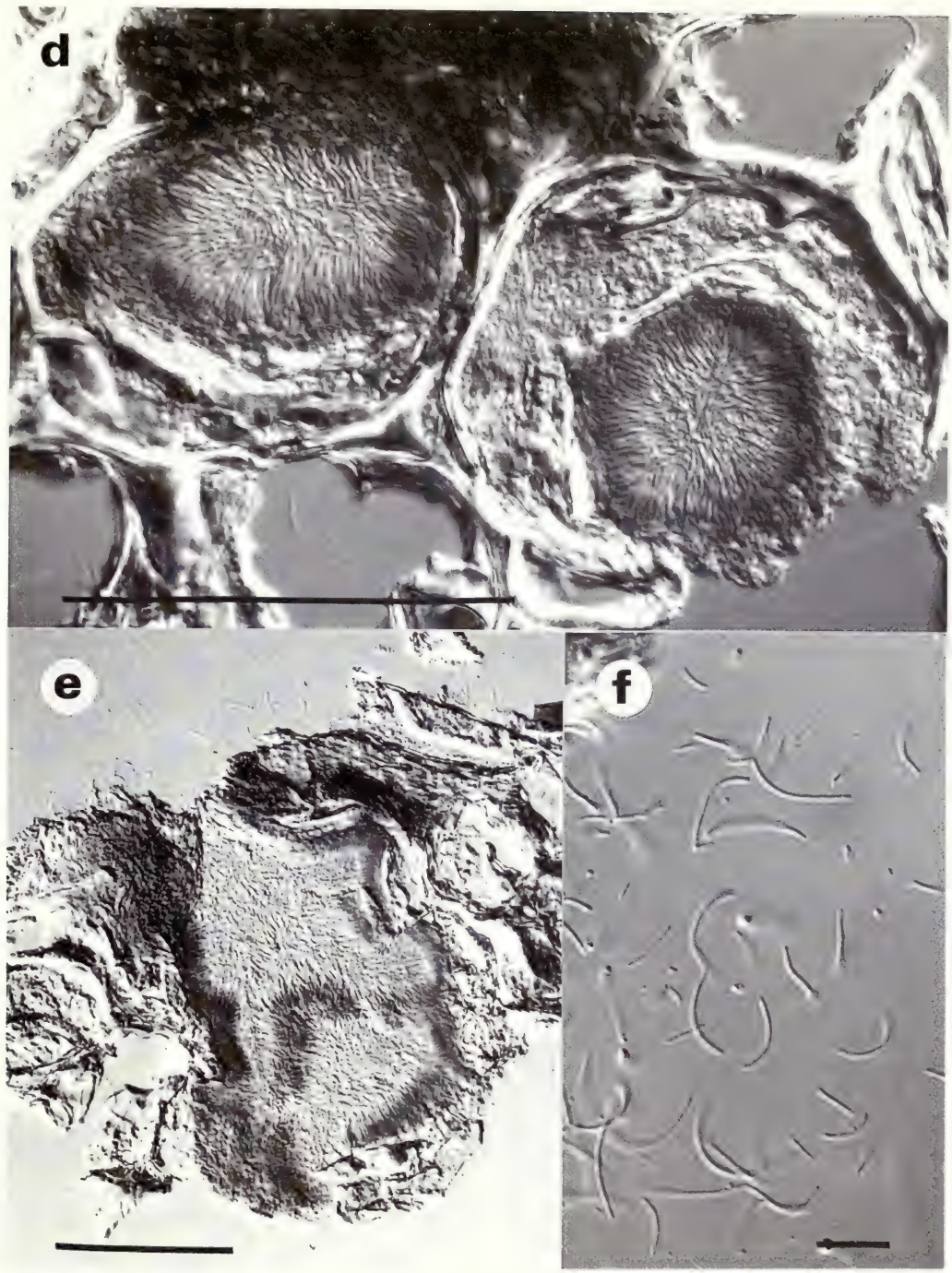


Fig. 40 *Celothelium stenobelum* (Nyl.) Aguirre (H–NYL 640–holotype) (d), (e) Vertical section of conidiomata; scale = 100 μm; (f) Conidia; scale = 10 μm.

support this, and the correct name seems to be *Celothelium stenobelum*.

C. stenobelum differs from the other species within the genus in its individual ascomata, with a centrally located ostiole, and stromatic conidiomata instead of pycnidial. This last characteristic made me hesitate as to whether to include this taxon in *Celothelium* or keep it apart. On the basis of having in common with the other taxa a higher number of features, e.g. ascomata structure, hamathecial development, ascus structure, ascus and ascospore morphology, conidiogenous cells and conidia morphology and development, at present the taxon is maintained in *Celothelium*.

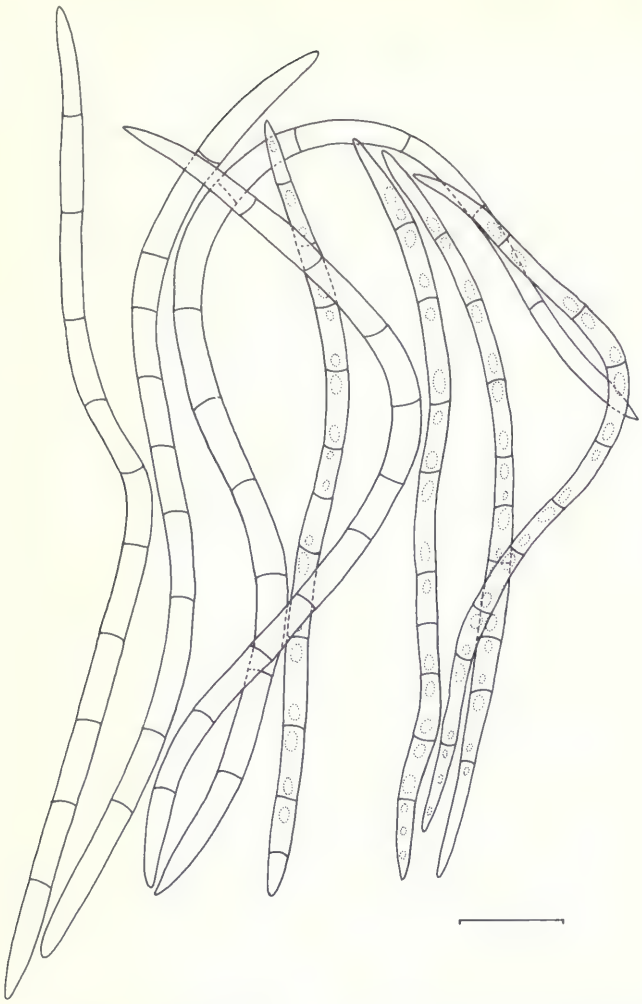


Fig. 41 Ascospore outlines of *Celothelium stenobelum* (Nyl.) Aguirre (H–NYL 640–holotype); scale = 10 μm.

IV **Cresporhaphis** Aguirre, **gen. nov.**

Leptorhaphis sect. *Integrae* Keissler, *Rabenh. Krypt., Fl.* **9**, 1(2): 241 (1938); nom. inval. (Art. 36.1).

Thallus epiphloeodes, versus immersus, tenuissimus, laevis ad pulveraceus, albido-cinerascens, nec continuus nec limitatus. *Photobiontus* chlorococcoideus. *Ascomata* perithecia similia, nigra, integra, laevia, solitaria ad confluentia, sessilia, conica ad ampuliformia, nucleo globosa; cum ostiolo centrali in brevi rostro locato. *Excipulum* atrobrunneum, KOH haud reagens, e textura angulari compositum, aliquando prismatica in locis et interdum obtecta per involucrellum. *Hamathecium* e paraphysibus compositum, interdum ramificantibus et anastomosantibus, 1.5–2 μm crassis, in gelatino immersis cum iodo sucineo ad veneto reagenti; canalis ostioli cum periphysibus incoloratis. *Asci* cylindrico-clavati, 8-spori, parietibus tenuibus, apicibus nonnihil incrassatis, aliquando pileatis, ab poro conico vel angustato sulcatis. *Ascosporae* distichae, incolores, falcatae, cum apicibus aliquando rotundatis, tenuis-murales, 09 transseptatae, sine strato gelatinoso. *Pycnidia* globosa, dispersa, nigra. *Conidia* incoloria, bacillariformia ad filiformia, simplicia, tenui-muralia.

Holotypus: *Cresporhaphis wienkampii* (Lahm) Aguirre [syn. *Leptorhaphis wienkampii* Lahm].

Thallus: Crustose, smooth to pulverulent, greyish-white, not continuous and not well delimited, immersed in the bark, composed of pale brown to colourless, thin-walled hyphae associated with globose chlorococcoid algae.

Ascomata: Perithecioid, black, smooth, individual to confluent, numerous, sometimes laterally collapsed; semi-immersed in the bark to superficial, conical to flask-shaped, with a central apical ostiole located in a short beak. Exciple: continuous, composed of a dark brown layer, not changing colour after 10% KOH treatment, becoming colourless towards the centrum, sometimes incorporating bark material on both sides of the ascomata to half the height; consisting of thick-walled, isodiametric to elongated cells, with elongated lumina and dark brown walls, forming a textura angularis, becoming radially compressed in places, reminiscent of a textura prismatica. A few species also have a covering dark brown involucrellum, sometimes incipient, not extending beyond the ascomata in a basal fringe; consisting, like the wall or exciple, of thick-walled isodiametric cells with enlarged lumina. Hamathecium: composed of colourless, smooth, sometimes branching and anastomosing, thin-walled filaments, 1.5–2 μm broad, with infrequent septa, enveloped in mucus; base of the ostiolar canal sometimes with periphyses, composed of colourless, thin-walled hyphae; hymenial gelatin bluish in iodine, but never deep blue. Asci: arising from the base of the ascoma, ripening sequentially; cylindrical-clavate, short-stalked, apparently unitunicate in structure, thin-walled, sometimes thickening at the apex, forming an apical cap, occasionally pierced by a narrow or conical pore, not changing colour in iodine; no other apical structures seen; 8-spored; ascus discharge not observed, in some species the empty asci show longitudinal creasing, probably opened by a circular pore or large split. Ascospores: biseriately arranged in the asci, sometimes in two bundles, colourless, thin-walled, smooth, falcate, up to 9-septate, not constricted at the septa, somewhat rounded at the apices, without appendages or gelatinous sheaths.

Conidiomata: When present, pycnidial, circular, black, shiny, smooth, scattered singly; immersed in the bark, becoming superficial, globose. Wall: dark brown, continuous, composed of few layers of thin- walled, more or less isodiametric cells, forming a textura globulosa to angularis. Conidiogenous cells: colourless, thin-walled, smooth, more or less lageniform, arising from colourless, isodiametric cells adjacent to the conidiomata wall. Conidiogenesis: apparently enteroblastic. Conidia: colourless, aseptate, thin-walled, smooth, bacilliform to filiform.

NUMBER OF SPECIES. Five species are accepted here, distinguished primarily by the size of the ascomata and ascospores, iodine reaction of the hymenial gelatin, the morphology of the ascus apex, and the ascomatal arrangement. However, it is likely that other species remain to be recognized.

ECOLOGY. On the bark of deciduous trees, mainly along the furrows and cracks, not causing any apparent damage; at least some species lichenized with chlorococcoid globose algae different from *Trentepohlia*.

DISTRIBUTION. At present only known from Europe.

OBSERVATIONS. This generic name partly honours the contribution to Spanish lichenology of my friend and colleague

Professor Ana Crespo, while I have retained the suffix '-*rhaphis*' (Gk ραφίς, needle) to indicate the connection with the genus *Leptorhaphis* within which the species referred here were formerly placed.

RELATIONSHIPS. It is difficult to refer this new genus satisfactorily to any systematic group until detailed studies on its ascomatal ontogeny have been carried out. Nevertheless, on the apical morphology of the asci as well as the characteristics of the hamathecium (branching paraphyses), the genus is reminiscent of some marginal groups of the Ostropales, such as *Xylopezia* Höhnel. However, *Xylopezia* appears to be ascolocular, and although their thick-walled asci do not look functionally bitunicate, they might have secondarily lost their bitunicate discharge mechanism (Sherwood-Pike & Boise, 1986). In the latter, a few species previously referred to *Zignoella* (Sacc.) Sacc., a genus without a clear position in the Trichosphaeriaceae (for nomenclatural discussion see Booth, 1958; Gams & Holubová-Jecková, 1976; Müller *in* Eriksson & Hawksworth, 1987*b*) were included in *Xylopezia* and *Mycowinteria*. Moreover, the genus *Cresporhaphis* has some morphological features, such as the ascomata and the asci, in common with *Chaetosphaeria* and the remaining species of *Zignoella*, such as *Z. ovoidea* (Fr.) Sacc. [syn. *Zignoina* Cooke; Müller *in* Eriksson & Hawksworth, 1987*b*], suggesting some affinities with the Trichosphaeriales (Barr, 1983: 11), like superficial and globose ascomata with periphysate ostiole, unitunicate asci, without apparent apical apparatus. However, I am not aware of the presence of any dematiaceous hyphomycetes or similar anamorphs, such as *Chloridium*, in *Cresporhaphis*, as reported by Gams & Holubová-Jecková (1976) for *Chaetosphaeria*, although pycnidial conidiomata have been observed in some of the species, bearing two conidia types: bacilliform microconidia (*Cresporhaphis acerina*, p. 000) and filiform macroconidia (*C. macrospora* and *C. wienkampii*, p. 000 & 000 respectively), apparently enteroblastically produced.

At present and until ontogenetic data are included, for the above characteristics it seems appropriate to refer *Cresporhaphis* to the Trichosphaeriales.

Key to the species

1. Ascospores aseptate, mostly less than 30 µm in length 2
– Ascospores 1- to multiseptate, mostly exceeding 30 µm in length 4

2(1). Ascomata confluent; hymenial gelatin bluish-amber in iodine; on trunks of *Acer* ..... 3. **C. muelleri**
– Ascomata solitary; hymenial gelatin bluish or not in iodine; on twigs of *Acer* or trunks of other deciduous trees 3

3(2). Ascomata semi-immersed in bark, 100–200 µm diam; hymenial gelatin unchanged in iodine; asci with a distinct apical cap pierced by a narrow and short pore; on twigs of *Acer* ..... 1. **C. acerina**
– Ascomata superficial, 150–300 µm diam; hymenial gelatin bluish-green in iodine; asci without an apical thickening; on trunks of *Salix*, *Robinia* or *Quercus* ..... 5. **C. wienkampii**

4(1). Ascospores 1-, 3-septate, 50–85 × 3–4.5 µm; on trunks of *Quercus* ..... 2. **C. macrospora**
– Ascospores 5-, 9-septate, 40–65 × 3–4 µm; on trunks of *Pinus* ..... 4. **C. pinicola**

The species

1. **Cresporhaphis acerina** (Rehm) Aguirre, **comb. nov.**

Leptorhaphis acerina Rehm in *Ber. naturhist. Ver. Augsburg* **26**: 51 (1881). Type: Germany, Bayern, 'ad corticem suberosam ramorum vivorum aceris camp. in sylva Franconiae bav.', 1870, H. Rehm, [Rehm *Ascomyceten* exs. no. 197] (S!—lectotype, selected here; K!, W 1923!, 1578!—isolectotypes).

Metasphaeria robergia Schulzer & Saccardo, *Revue mycol.* **6**: 70 (1884). Type: Yugoslavia, Crni Gaj Wood, 'in cortice *Aceris campestris*, pr. Vinkovce' (W 247!—holotype, illustration [Art.7.3]).

Fig. 42, 43A.

Thallus: Immersed in the bark, composed of pale brown to colourless, undulating, thin-walled, smooth, cylindrical hyphae, branching dichotomously, constricted at the septa, 2–4 µm wide, associated with globose chlorococcoid algae, 6.5–9 µm diam.

Ascomata: Perithecioid, circular, black, shiny, smooth, scattered singly, 100–200 µm diam; conical to hemispherical, immersed in bark to half their height, with a central apical ostiole. Exciple: continuous, composed of two differently coloured layers: the outer dark brown, 12–24 µm thick, tending to be thicker in its upper part, sometimes incorporating bark material in its lower part, composed of thin-walled cells, 2.5–7.5 µm diam, with an enlarged lumen and dark brown walls, forming a textura angularis, sometimes radially compressed and becoming almost prismatica in the lower part; the inner layer colourless to pale brown, 12–16 µm, directly adjacent to the centrum, composed of colourless cells similar to those of the outer layer, but slightly smaller, not sharply distinguished from, but intergrading with the outer wall. Hamathecium: composed of colourless, smooth, occasionally branched, thin-walled hyphae, less than 2 µm wide, with infrequent septa, enveloped in mucus; hymenial gelatin not changing colour in iodine; periphyses not observed. Asci: cylindrical, short-stalked, apparently 'unitunicate', 65–80 × 6–8.5 µm, thin-walled, with a distinct thickening at the apex, pierced by a narrow and short pore, not changing colour in iodine, but staining dark blue in cotton-blue; no other apical structures seen; 8-spored. Ascospores: biseriately arranged in the ascus, colourless, thin-walled, smooth, falcate, aseptate, 20–27 × 2.5–3.5 µm, without appendages.

Conidiomata: Pycnidial, black, matt, smooth, circular, scattered singly, *c.* 30 µm diam and always present intermixed with the ascomata; totally immersed in the bark, globose. Wall: continuous, dark brown, 7–8 µm thick, composed of thin-walled cells, 3–5.5 µm diam, with enlarged lumina and dark brown walls, forming a textura globulosa. Conidiogenous cells: colourless, thin-walled, smooth, more or less lageniform, *c.* 5 × 2.5 µm, arising from colourless cells adjacent to the conidiomatal wall. Conidiogenesis: apparently enteroblastic. Conidia: colourless, aseptate, thin-walled, smooth, bacilliform, 3.5–4 × 1 µm.

ECOLOGY. On twigs of *Acer campestre* L., mainly along the bark furrows, and not causing any apparent damage; probably lichenized, associated with unidentified globose chlorococcoid algae.

DISTRIBUTION. Europe, Germany and Yugoslavia. Only known from type localities.

TYPIFICATION. Rehm's exsiccates have been widely distributed, and in many cases there is no clear holotype. The

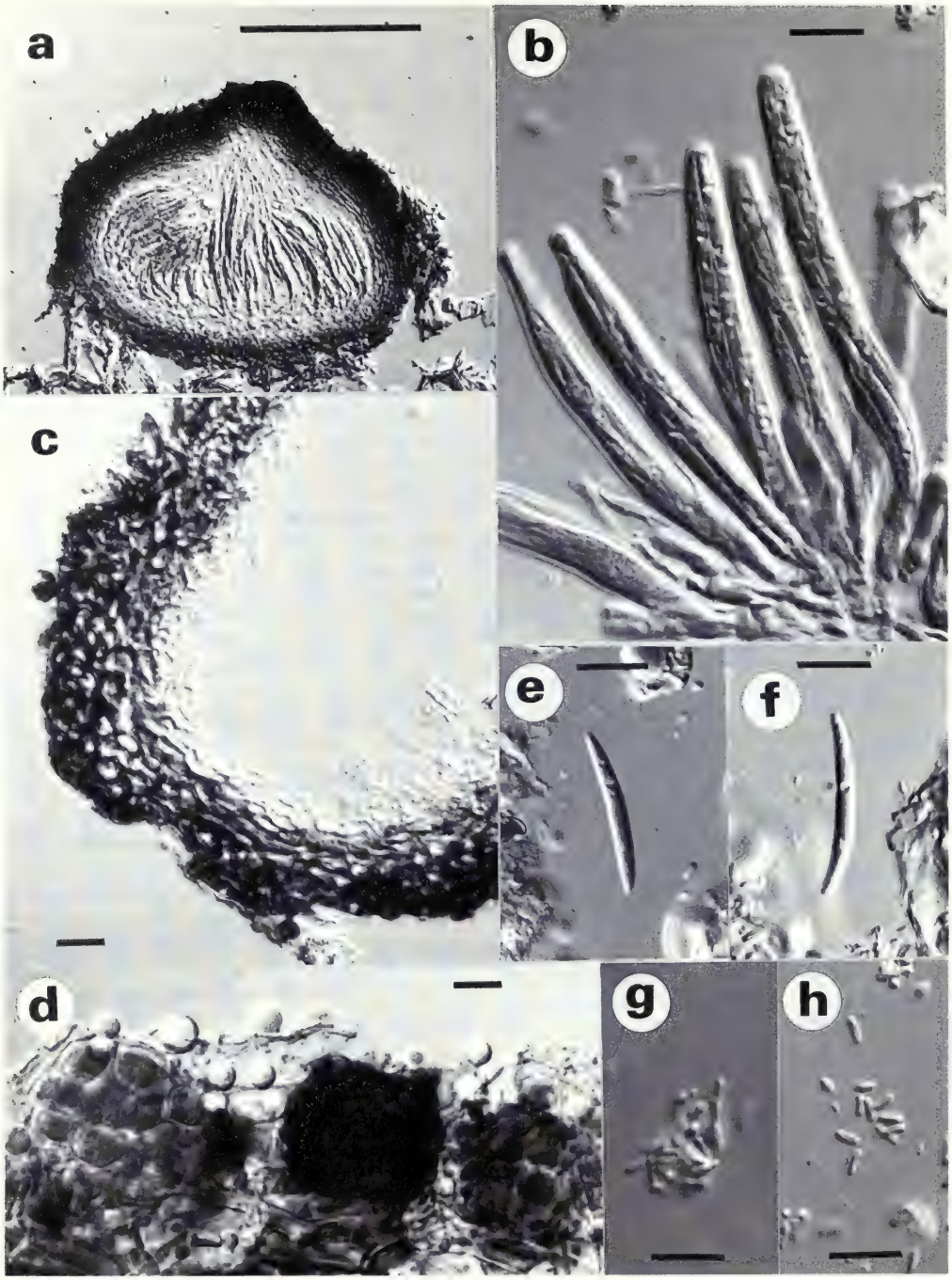


Fig. 42 *Cresporhaphis acerina* (Rehm) Aguirre (S–lectotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Asci and ascospores; (c) Detail of exciple: textura angularis; (d) Detail of photobiont and conidiomata; (e), (f) Ascospores; (g) Conidiogenous cell; (h) Conidia; scale = 10 μm.

material in Rehm's herbarium, now in S, which is part of the original collection, is selected as the lectotype for *C. acerina* here.

The type material of *Metasphaeria robergia* is missing from W. Instead, I obtained a photocopy of Schulzer's manuscript 'Pilze aus Slavonien', which includes, as reported by Keissler (1938), an illustration of the fungus, and this is here accepted as the holotype (Art.7.3).

OBSERVATIONS. The illustration of *Metasphaeria robergia* shows that the taxon clearly belongs to *Cresporhaphis*, and it is placed here as a synonym of *C. acerina* on the basis of their similar ecology, both growing on *Acer campestre*, and their individual ascomatal arrangement, and thus differs from *C. muelleri* with confluent ascomata, also found on *Acer* bark. Schulzer, however, described the fungus as having bigger ascospores (36–48 × 3 μm). Keissler (1938: 244) placed this

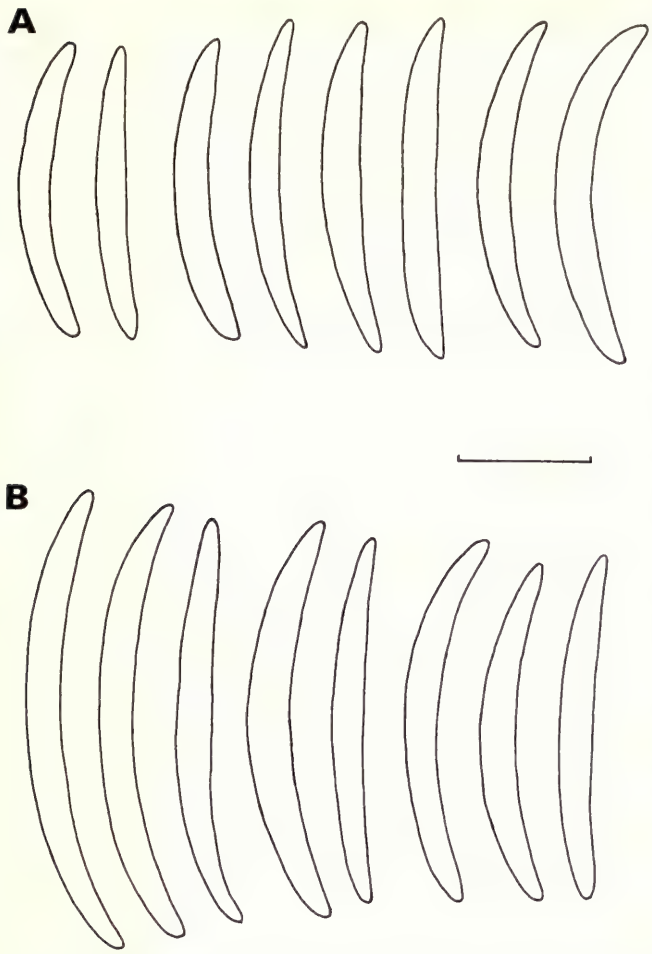


Fig. 43 Ascospore outlines (A) *Cresporhaphis acerina* (Rehm) Aguirre (W–isolectotype); (B) *Cresporhaphis muelleri* (Duby) Aguirre (W 3522/4155–holotype of *Leptorhaphis aggregatus*); scale = 10 μm.

taxon, together with *C. muelleri* and *C. acerina*, as a synonym of *C. wienkampii*. These taxa are different species according to their ascomatal structure and size, as well as varying in the thickening of the ascus apex and ascospore sizes.

2. **Cresporhaphis macrospora** (Eitner) Aguirre, **comb. nov.**

Leptorhaphis quercus f. *macrospora* Eitner in *Jber. schles. Ges. vaterl. Kult.* **78**(2b): 25 (1901) ['1900']. Type: Poland, Silesia, 'Neinptoch Kl. Elguth', on *Quercus robur*, 12 April 1892, *E. Eitner* (W 19701!—lectotype, selected here).

Fig. 44, 45.

Thallus: Pulverulent, whitish, shiny, not continuous and not well delimited; superficial to immersed in the bark, compose of colourless to dark brown, thin-walled, smooth and cylindrical hyphae, less than 3 μm wide, frequently septate and not constricted at the septa, branching dichotomously, superficially associated with globose chlorococcoid algae, *c.* 10 μm diam, and intermixed with bark material.

Ascomata: Perithecioid, black, smooth, individually scattered, on occasion confluent, numerous, sometimes collapsed laterally, 250–300 μm wide; half-immersed in the substratum, flask-shaped, 300–350 μm tall, with a central ostiole in a short beak. Exciple: continuous, dark brown, becoming colourless towards the centrum, 20–30 μm thick, incorporating bark material on both sides of the ascomata to half the height; consisting of thin-walled, isodiametric to elongated cells, 4–8 μm diam, with elongated lumina and dark brown walls, forming a textura angularis. Hamathecium: composed of colourless, smooth, occasionally branching, thin-walled filaments, *c.* 1.5–2 μm wide, with infrequent septa, enveloped in mucus; base of the ostiolar canal with colourless, thin-walled hyphae, less than 2 μm diam, infrequently septate, not constricted at the septa and unbranched, shorter than the paraphyses; hymenial gelatin unchanged in iodine. Asci: clavate to subcylindrical, short-stalked, 115–155 × 10–15 μm, apparently unitunicate, with a thin wall, thickened at the apex in young asci, apical cap pierced by a broad conical pore, not turning blue in iodine; no other apical structures seen; 8-spored. Ascospores: biseriately arranged in the asci, sometimes in two bundles, colourless, thin-walled, smooth, falcate, 1-, 3-septate, 50–85 × 3–4.5 μm.

Conidiomata: Pycnidial, black, shiny, smooth, scattered singly, *c.* 100–150 μm diam; immersed in the bark, but becoming superficial, globose. Wall: continuous, dark brown, *c.* 10 μm thick, composed of few layers of thin-walled cells, 3–5.5 μm diam, with enlarged lumina and dark brown walls forming a textura globulosa. Conidiogenous cells: colourless, thin-walled, more or less lageniform, *c.* 12 μm in length, arising from colourless, isodiametric cells, 3.5–4.5 μm diam, adjacent to the conidiomatal wall. Coniodiogenesis: apparently enteroblastic. Conidia: colourless, aseptate, thin-walled, smooth, filiform and curved, 25–30 × 1 μm.

ECOLOGY. On rough bark of *Quercus robur* L., along the furrows with lichenized fungi such as species of *Parmelia*, *Xanthoria*, and *Lecanora*, not causing any apparent damage; probably lichenized with unidentified chlorococcoid algae.

DISTRIBUTION. Probably widespread in central Europe in the last century and beginning of the present century; also known from Sweden. I am not aware of any recent collections, but it might be expected in other temperate regions of the Northern Hemisphere.

TYPIFICATION. Eitner collected several specimens before 1901, the date when the new taxon was effectively published, but he did not designate an holotype; neither did he mention the type locality in the protologue. From the various specimens of Eitner's in W, W 19701 is selected as the lectotype here as it was in particularly good condition and well documented.

OBSERVATIONS. This species was described as a form of *Leptorhaphis quercus* Beltram., and has also been mistaken for it. According to Beltramini's (1858) description and illustrations of that species these fungi are not closely related; they differ in the structure of the ascomata, hamathecial tissues, and ascus structure (see 'Excluded species', p. 178). This form is consequently recognized at the rank of species here. *C. macrospora* differs from the other species included in the genus in the larger asci and ascospores, the clavate asci, and septate ascospores. One other species of this genus, *C. pinicola* (G. Samp.) Aguirre, also has septate ascospores, but in that species they are usually 5-, 7-septate, whereas in *C. macrospora* they are only 1-, 3- septate.

ADDITIONAL SPECIMENS. **Austria**, Carinthia, Klagenfürt, *J. Steiner* (W 1594). Carinthia, Sieben Hügeln, Klagenfurt, 'ad

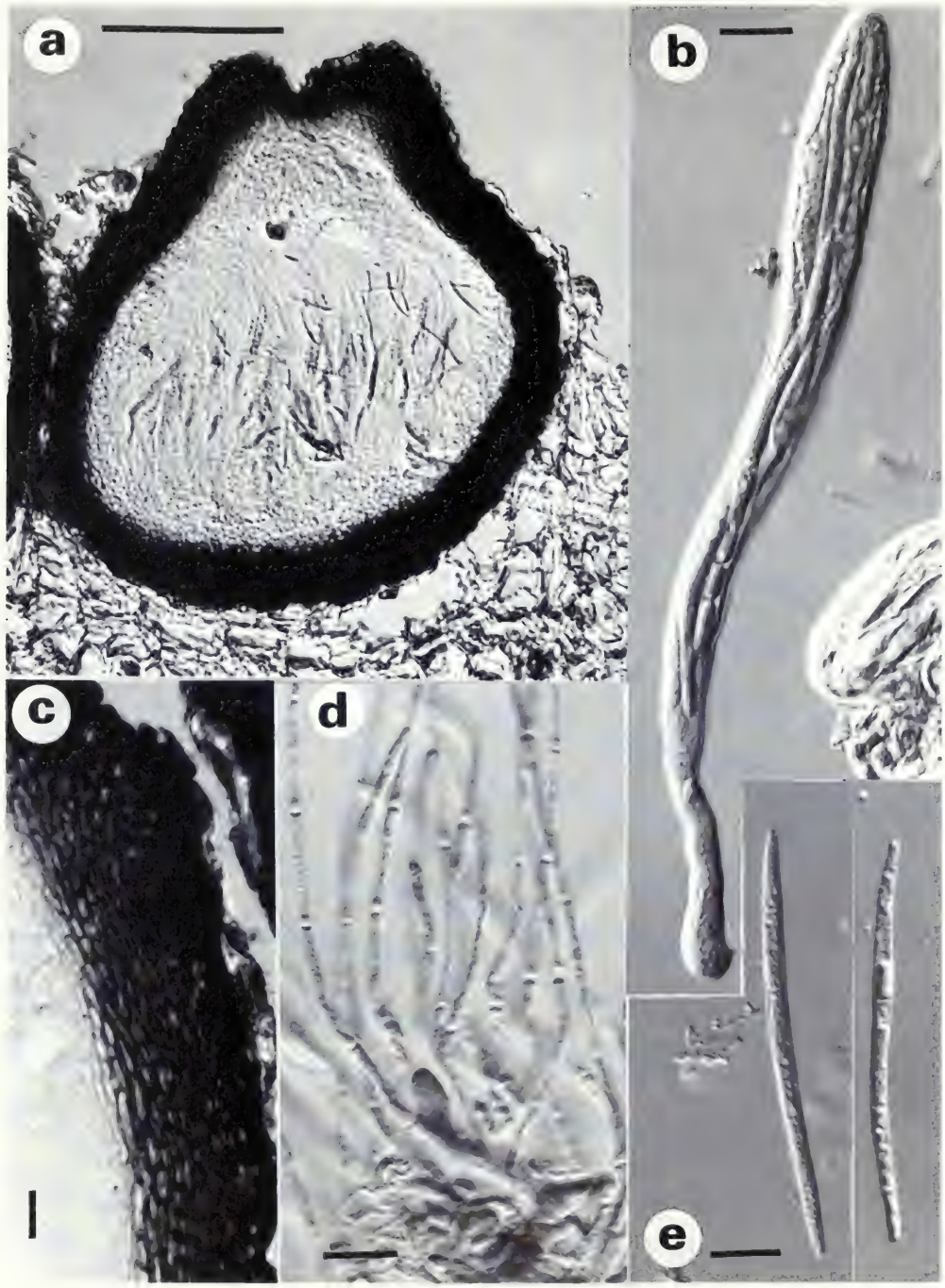


Fig. 44 *Cresporhaphis macrospora* (Eitner) Aguirre (W 19701–lectotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Ascus and ascospores biseriately arranged; (c) Detail of exciple: textura angularis to prismatica; (d) Paraphyses; (e) Ascospores; scale = 10 μm.

truncos *Quercuum* in collibus', *J. Steiner* [Zahlbr., *Lich. rar. exs.* no. 131 as *Leptorhaphis quercus*] (PAD, BM, B 59602). **Germany**, Nordrhein-Westfalen, Greven, September 1862, *W. Fuisting* (B 59591); loc. cit., on *Quercus*, 1 September 1862, *W. Fuisting* (B 59599). München, 1864, *W. Fuisting* (B 59590). Niedersachsen, Ibùrg, Grùvetar, September 1862, *T. R. J. Nitschke* (B 59631). **Hungary**, Szobrany, *F. A. Hazslinsky* (BM). **Poland**, Silesia ... [illegible] 'an jüngerer ... [illegible] im Wald ... [illegible] Roswaere & Teszona', 26 March 1892, *E. Eitner* (W 4156). Silesia, Wroclaw, Obernigk, on *Quercus robur*, 27 April 1896, *E. Eitner* (BM). Silesia, Minkowskiér wald, on *Quercus*, 13 August 1892, *E. Eitner* (B 33574). **Sweden**, Närke, *P. B. Hellbom* (BM–2 specimens). **Switzerland**, Zürich, 1887, *C. Hegetschweiler* (B 59705). **Yugoslavia**, '... [illegible] Bach, ... [illegible] bei klugerbach', on *Quercus robur*, *J. Steiner* (W 19628).

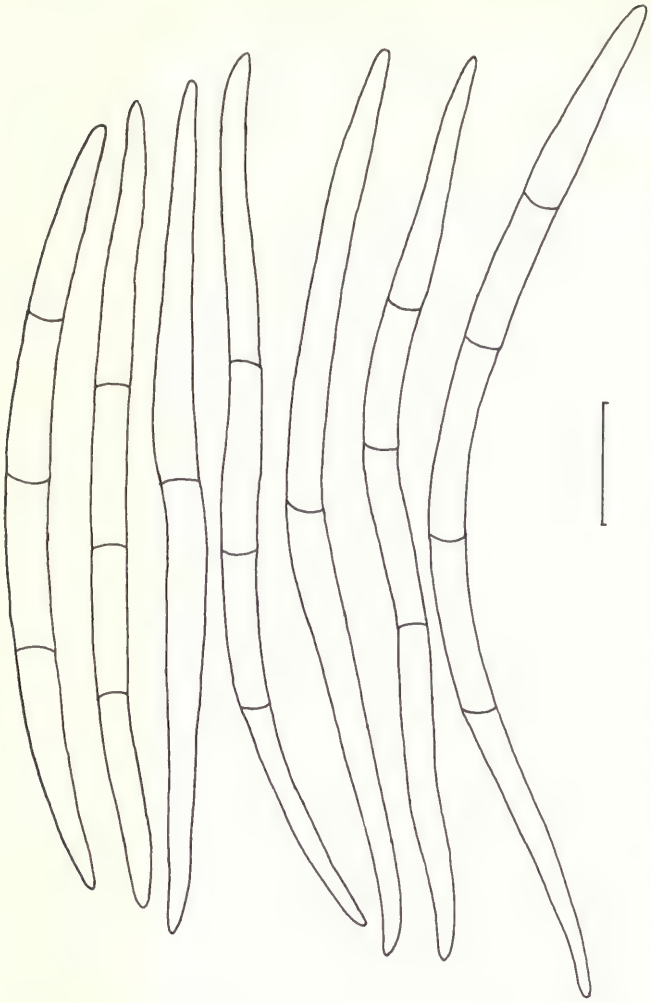


Fig. 45 Ascospore outlines of *Cresporhaphis macrospora* (Eitner) Aguirre (W 19701–holotype, W 4156); scale = 10 μm.

3. **Cresporhaphis muelleri** (Duby) Aguirre, **comb. nov.**

Sphaeria muelleri ['Mülleri'] Duby *in* Klotzsch, *Herb. Mycol.*, Ed. II, ser. 1, no. 642 (1857)., *Leptosphaeria muelleri* (Duby) Auersw. *in* Gonnerman & Rabenhorst *Mycol. Europ.* **5**, t. 12, f. 167 (1869). Type: France, Haute Savoie, Les Contamines, 'ad corticem squamosam Aceris', *J. Müller Argoviensis* [Klotzsch, *Herb. Mycol. exs.* no. 642] (K!—lectotype, selected here).

Leptorhaphis aggregatus Eitner in *Jber. schles. Ges. vaterl. Kult.* **78**(2): 25 (1901) ['1900']. *Leptorhaphis wienkampii* var. *aggregata* (Eitner) Keissler, *Rabenh. Krypt., Fl.* **9**, 1(2): 246, fig. 82 (1938). Type: Poland, Silesia, Riesengebirge, Glatz-Reinerz, Seefelder, Pischkowitz, on *Acer pseudoplatanus*, August 1896, *E. Eitner* (W 3522/4155!—holotype).

Fig. 43B, 46.

Thallus: Greyish-white, shiny, not continuous and not well delimited; superficial to immersed in the bark, composed of colourless to pale brown, thin-walled, smooth, cylindrical hyphae, constricted at the septa, less than 3 μm wide, associated on the surface with globose chlorococcoid algae, *c.* 7–11 μm diam.

Ascomata: Perithecioid, black, matt, smooth, usually confluent, irregular in shape, *c.* 1 mm long, emerging from cracks on the surface of the bark, flask-shaped when solitary, 300–400 μm diam; immersed in the bark to half their height; ostiole centrally located in a short beak. Exciple: continuous, composed of two differently coloured layers: the outer wall dark brown to black, incorporating bark material in both sides and in contact with the annexe ascomatal wall, 25–45 μm thick, forming a pseudostroma and surrounding the inner wall, composed of thin- walled isodiametric cells, 2.5–5.5 μm diam, with enlarged lumina and dark brown walls, forming a textura angularis; inner layer thinner, colourless to brownish, intergrading with the outer wall, directly adjacent to the centrum, composed of colourless to brown cells, similar to those of the outer layer but slightly smaller and radially compressed, forming a textura angularis, becoming prismatica in places. Hamathecium: composed of colourless, smooth, occasionally branched, thin-walled hyphae, *c.* 1–1.5 μm wide, septa infrequent, enveloped in mucus, hardly staining in cotton-blue; periphyses present, composed of colourless, thin-walled and short hyphae; hymenial gelatin bluish in iodine. Asci: cylindrical, short-stalked, 70–85 × 6–8.5 μm, apparently unitunicate, with a thin wall, thickened at the apex in young asci, cap slightly pierced by a short pore, becoming thinner when the ascospores have developed; apex not changing colour in iodine; no other apical structures seen; 8-spored; ascus discharge mechanism not observed, but empty asci show longitudinal creasing. Ascospores: biseriately arranged in the asci, colourless, thin-walled, smooth, falcate, aseptate, 25–30 × 2–3.5 μm.

Conidiomata: Not observed.

ECOLOGY. On undiscoloured bark of *Acer pseudoplatanus* L., mainly erumpent through small cracks in the bark, with an unidentified species of *Micarea* and bryophytes, not causing any apparent damage; probably lichenized with globose chlorococcoid algae.

DISTRIBUTION. Central Europe (France, Poland, and Germany), only known from old collections.

TYPIFICATION. The exsiccate of Klotzsch's *Herb. Mycol.* is widely distributed and contain descriptions, but I have only seen material of *Sphaeria muelleri* Duby from K, which is selected as the lectotype here. To my knowledge there is only one collection of *Leptorhaphis aggregatus*, in W, which is taken to be the holotype.

OBSERVATIONS. The species can be separated from the other taxa included in the genus by its ecology and in having confluent ascomata. Following these criteria, Keissler (1938) transferred the species to the rank of variety of *C. wienkampii*. The material of the species available showed that certain features such as the presence of an apical cap pierced by a pore, narrow ascospores and confluent ascomata seem sufficient to recognize the taxon at the rank of species. *C. muelleri* and *C. acerina* share that characteristic ascus cap, but differ in ascospore size, iodine reaction and ecology. Material of *C. muelleri* studied was always from trunks of *Acer*, whereas *C. acerina* is common on the twigs and branches.

ADDITIONAL SPECIMENS. **Germany**, Schwarzwald, Baden, St. Blasien, on *Acer*, 3 May 1914, *G. Lettau* (B 59692); loc. cit., Aitern-Mutten, near Schönan, 700–800m, on *Acer*, 28 June 1914, *G. Lettau* (B 59690). **Switzerland**, Graubunden, Oberhalbstein, 'Verorlberg: Oberhalb Partenen', on *Acer* . . . [illegible], 10 July 1907, *G. Lettau* (B 59688).

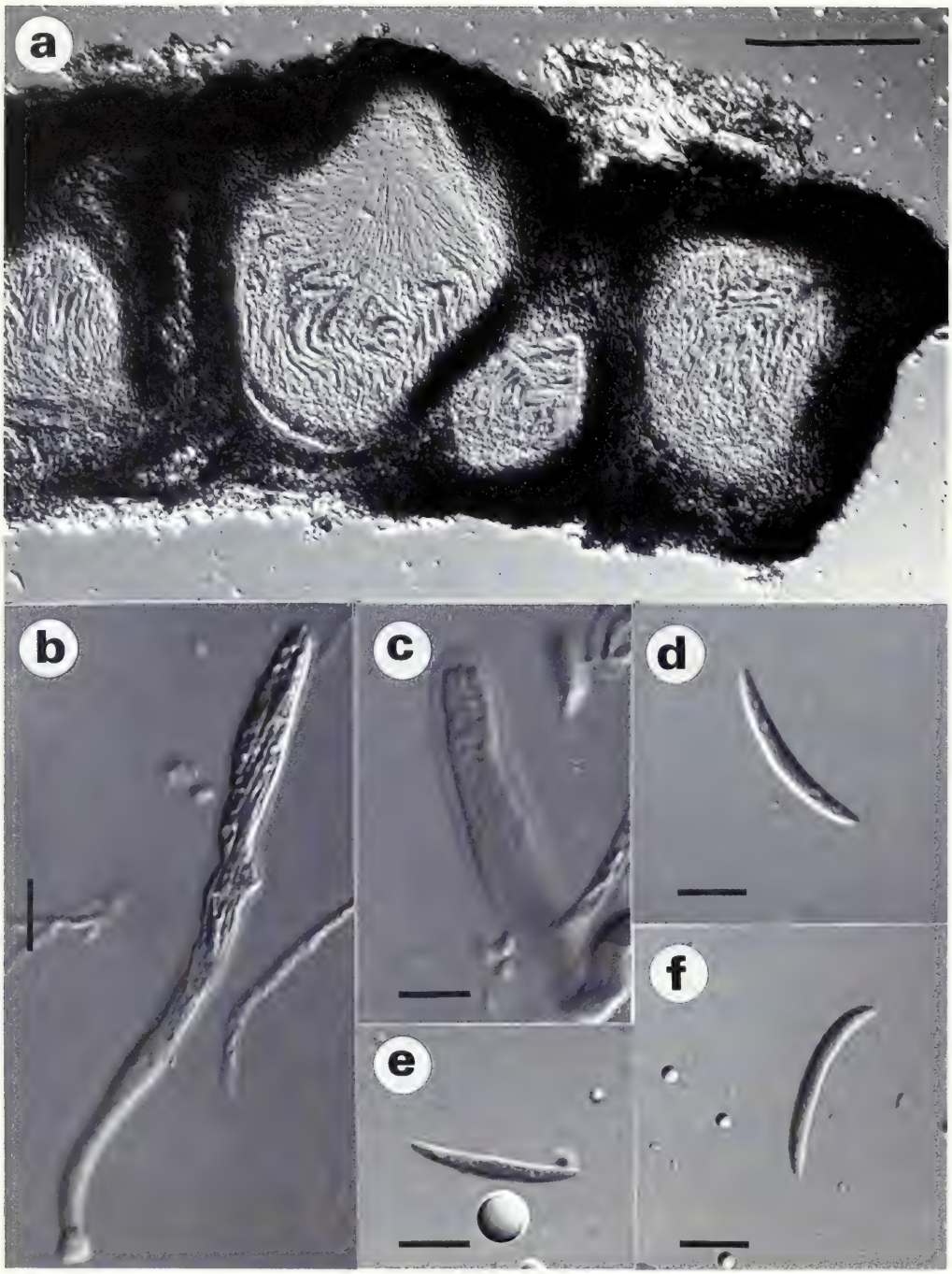


Fig. 46 *Cresporhaphis muelleri* (Duby) Aguirre (W 3522/4155–holotype of *Leptorhaphis aggregatus*) (a) Vertical section of ascomata showing arrangement in common stroma; scale = 100 μm; (b) Ascus and ascospores; (c) Detail of ascus apex, slightly pierced by conical pore; (d), (e), (f) Ascospores; scale = 10 μm.

4. **Cresporhaphis pinicola** (G. Samp.) Aguirre, **comb. nov.**

Leptorhaphis pinicola G. Samp. in *Bolm Soc. broteriana* II, **2**: 163 (1924)., Type: Portugal, Estremadura, Sierra de Sintra; Castelo dos Mouros, 'sobre o ritidoma de *Pinus* sp.', 11 April 1943, *C. Tavares* (LISU 511!—neotype, selected here; UPS—isoneotype).

Fig. 47, 48.

Thallus: Ash-grey, smooth, matt, not continuous and not well delimited; mainly superficial, composed of colourless to dark brown, thin-walled, smooth, cylindrical hyphae, constricted at the septa, 2–3.5 μm diam, associated with globose chlorococcoid algae, *c.* 7.5–12 μm diam.

Ascomata: Perithecioid, black, shiny, smooth, scattered singly, 200–300 μm diam, globose to flask-shaped, usually superficial with a central apical ostiole. Involucrellum: dark

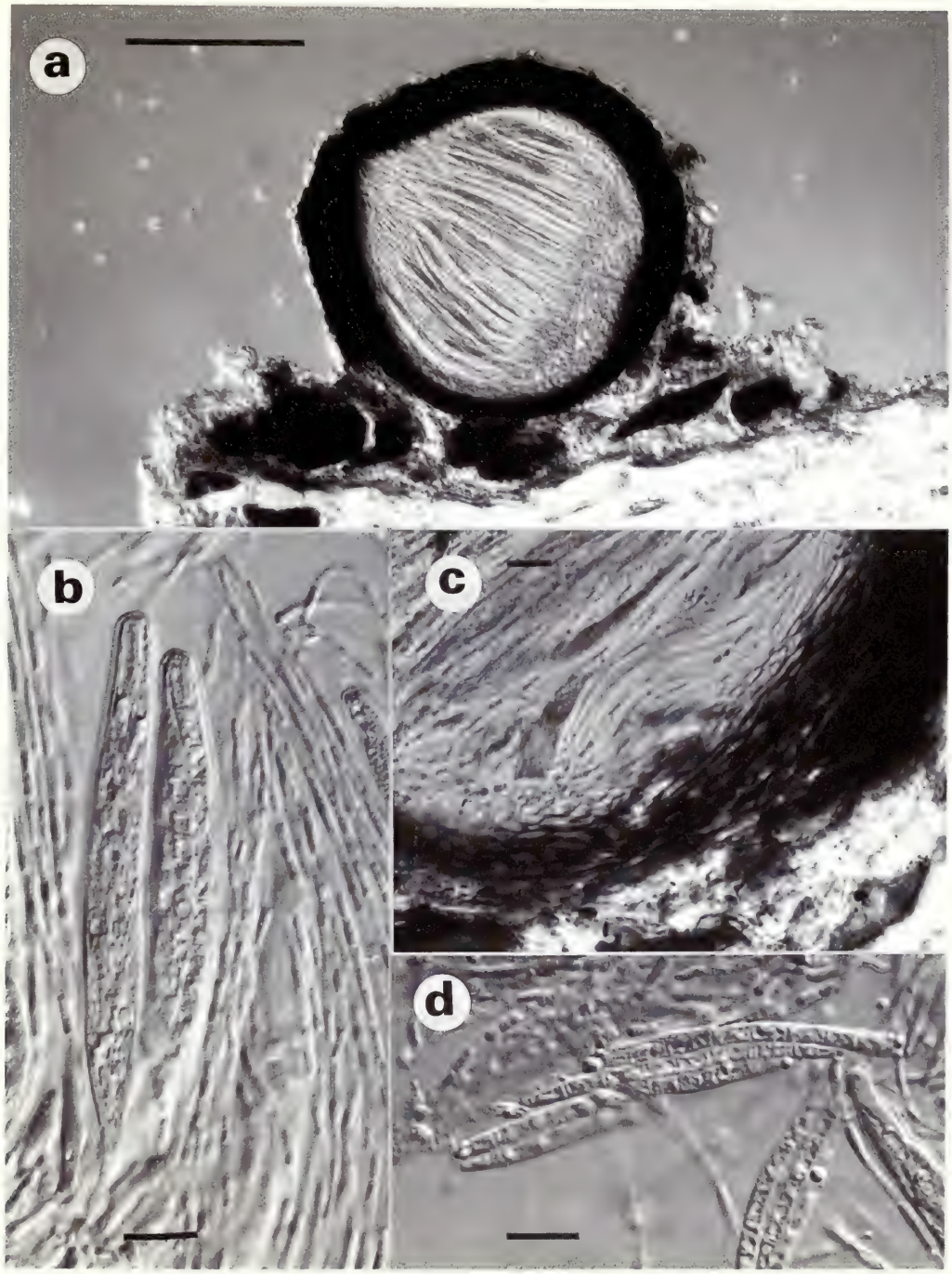


Fig. 47 *Cresporhaphis pinicola* (G. Samp.) Aguirre (LISU 511–neotype) (a) Vertical section of ascoma, showing involucrellum; scale = 100 μm; (b) Asci, ascospores and paraphyses; (c) Detail of exciple: textura angularis to prismatica; (d) Ascospores; scale = 10 μm.

brown, *c.* 25 μm thick, slightly extending beyond the ascomata but not forming a proper fringe. Exciple: continuous, dark brown, *c.* 20 μm thick, becoming colourless towards the centrum; both involucrellum and exciple composed of more or less isodiametric cells 3.5–5.5 μm diam, thick-walled with enlarged lumina, dark brown walls forming a textura angularis becoming pale brown Xto colourless and radially compressed towards the centrum, forming a textura angularis almost prismatica. Hamathecium: composed of colourless, smooth, thin-walled hyphae, less than 2 μm wide, infrequently septate, not constricted at the septa, occasionally branching, enveloped in mucus; periphyses, composed of colourless, smooth, thin-walled hyphae, *c.* 1.5–2 μm broad; hymenial gelatin unchanged in iodine. Asci: cylindrical, short-stalked, *c.* 80 × 8 μm, apparently unitunicate in structure, thin-walled, thickened at the apex, forming a small cap, not changing colour in iodine; no other apical structures seen; 8-spored. Ascospores: biseriately arranged in the asci, colourless,

thin-walled, smooth, acicular, sometimes falcate, 40–65 μm × 3–4 μm, 5-, 9-septate, not constricted at the septa.

Conidiomata: Not observed.

ECOLOGY. Growing on *Pinus* bark with *Porina leptalea* (Durieu & Mont.) A. L. Sm. and *Trentepohlia* sp., not causing any apparent damage; probably lichenized, associated with chlorococcoid algae.

DISTRIBUTION. Europe, Portugal. Only known from the type locality.

TYPIFICATION. The type material [Sintra, Estefaniá,'quinta dos platanos, nos pinheiros', January 1922, *A. Ricardo Jorge*] was requested from PO where Sampaio's herbarium is now kept, but could not be found (PO; Prof. R. Salema, in litt.). Instead I obtained material from the same locality, collected by C. Tavares (1943), from UPS and LISU which fits very well with the description provided by Sampaio (1923) in the protologue. Since the holotype or type material appears to be lost, LISU 511 is here designated as the neotype to replace it.

OBSERVATIONS. This species differs from the other taxa included in the genus *Cresporhaphis* particularly in the length and septation of the ascospores (usually 5–9 septa) and other characteristics such as the presence of a differentiated involucrellum, asci size and colour of the thallus. There is no mention of the taxon in recent European lichen-floras such as Clauzade & Roux (1985).

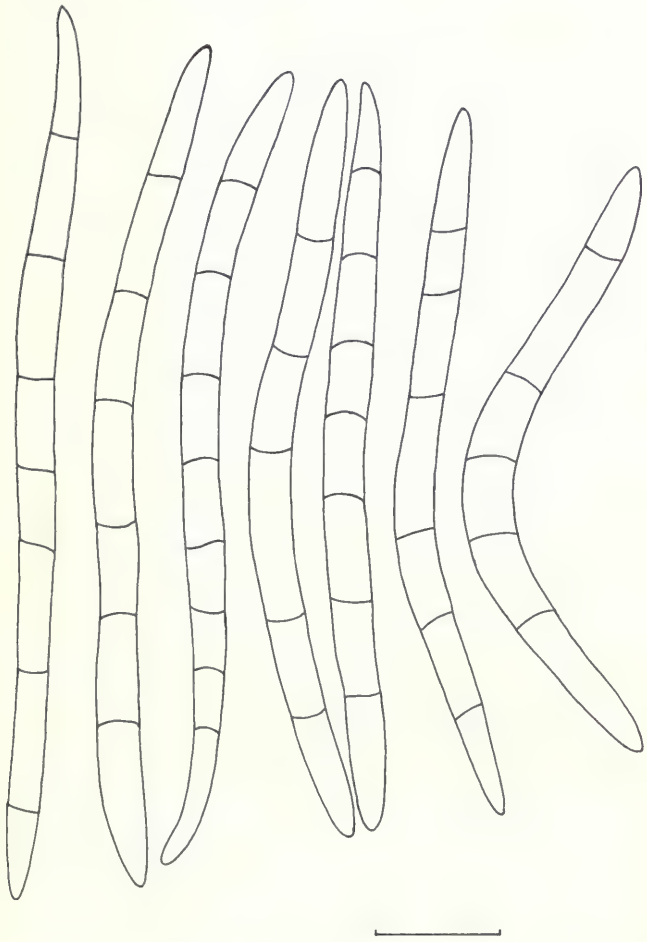


Fig. 48 Ascospore outlines of *Cresporhaphis pinicola* (G. Samp.) Aguirre (LISU 511–neotype); scale = 10 μm.

5. **Cresporhaphis wienkampii** (Lahm ex Hazslin) Aguirre, **comb. nov.**

Leptorhaphis wienkampii Lahm ex Hazslin in *Verh. Ver. Nat., Heilk. Pressburg* **5**: 12 (1861). Type: Germany, Westfalen, Münster, Handorf, on bark of *Salix fragilis*, 1862, *P. Wienkamp* [Rabenhorst, *Lich. europ. exs.* no. 651, as *Leptorhaphis wienkampii*] (L!—neotype, selected here; BM!—2 isoneotypes).

Fig. 49, 50.

Thallus: Very thin, only apparent in vertical section, composed of pale brown to colourless, undulating, thin-walled, smooth, cylindrical hyphae, 2.5–4 μm wide, associated with globose, chlorococcoid algae, *c.* 4.5–6.5 μm diam, and mixed with bark cells.

Ascomata: Perithecioid, globose to flask-shaped, sometimes laterally collapsed, black, shiny, smooth, superficial, scattered singly, 150–300 μm diam, flattened when mature, saucer-like, 270–325 μm in height; ostiole central, in a short beak. Exciple: continuous, composed of two coloured layers, the outer dark brown, 25–40 μm thick, incorporating bark material in its lower part, composed of thin-walled cells, isodiametric to laterally compressed, 4–8 μm × 2–4 μm, with enlarged lumina and dark brown walls, forming a textura angularis; the inner layer pale brown to colourless, thinner, directly adjacent to the centrum, composed of brown to colourless cells, similar to those of the outer layer, but slightly smaller, forming also a textura angularis. Hamathecium: composed of colourless to hyaline, smooth, occasionally branching, thin-walled hyphae, less than 2 μm wide, with infrequent septa, enveloped in mucus and free at the tips; periphyses, colourless, smooth, thin-walled, unbranched hyphae, less than 2 μm wide; hymenial gelatin bluish-green in iodine. Asci: subcylindrical to clavate, short- stalked, 80–120 μm × 8–14 μm, apparently 'unitunicate', with a thin wall, without an apical thickening; apex not changing colour in iodine; no other apical structures seen; 8-spored. Ascospores: biseriately arranged in the asci, colourless, thin-walled, smooth, falcate, (20–) 25–30 (–35) × 3–3.5 μm, aseptate, occasionally 1-, 3-septate, with several refringent particles.

Conidiomata: Pycnidial, circular, black, matt, smooth, scattered singly, *c.* 140 μm diam; immersed in the bark, globose. Wall: continuous, dark brown, nearly black, 10–15 μm thick, composed of thin-walled, isodiametric cells, *c.* 3.5–5.5 μm diam, with enlarged lumina, forming a textura angularis to globulosa. Conidiogenous cells: colourless, thin-walled, smooth, more or less lageniform, *c.* 10 μm in length, arising from colourless cells adjacent to the conidiomatal wall. Conidiogenesis: apparently enteroblastic. Conidia: colourless, aseptate, thin-walled, smooth, cylindrical to filiform, curved, 20–25 μm × 1 μm.

ECOLOGY. On rough bark of *Salix*, *Robinia pseudoacacia* L., *Quercus robur* L. and other trees, mainly along the bark furrows, with other lichens and fungi such as *Lecidella elaeochroma* (Ach.) M. Choisy, *Lecanora chlarotera* Nyl., and *Rebentischia unicaudata* (Berk. & R. Br.) Sacc., not causing any apparent damage; probably lichenized, associated with unidentified chlorococcoid algae.

DISTRIBUTION. From the exsiccata and other collections kept in different herbaria it is possible to observe that the fungus was probably widely distributed in central Europe, especially Germany, Poland, and Czechoslovakia, but also in Norway and Sweden. Nevertheless, no recent collections are known.

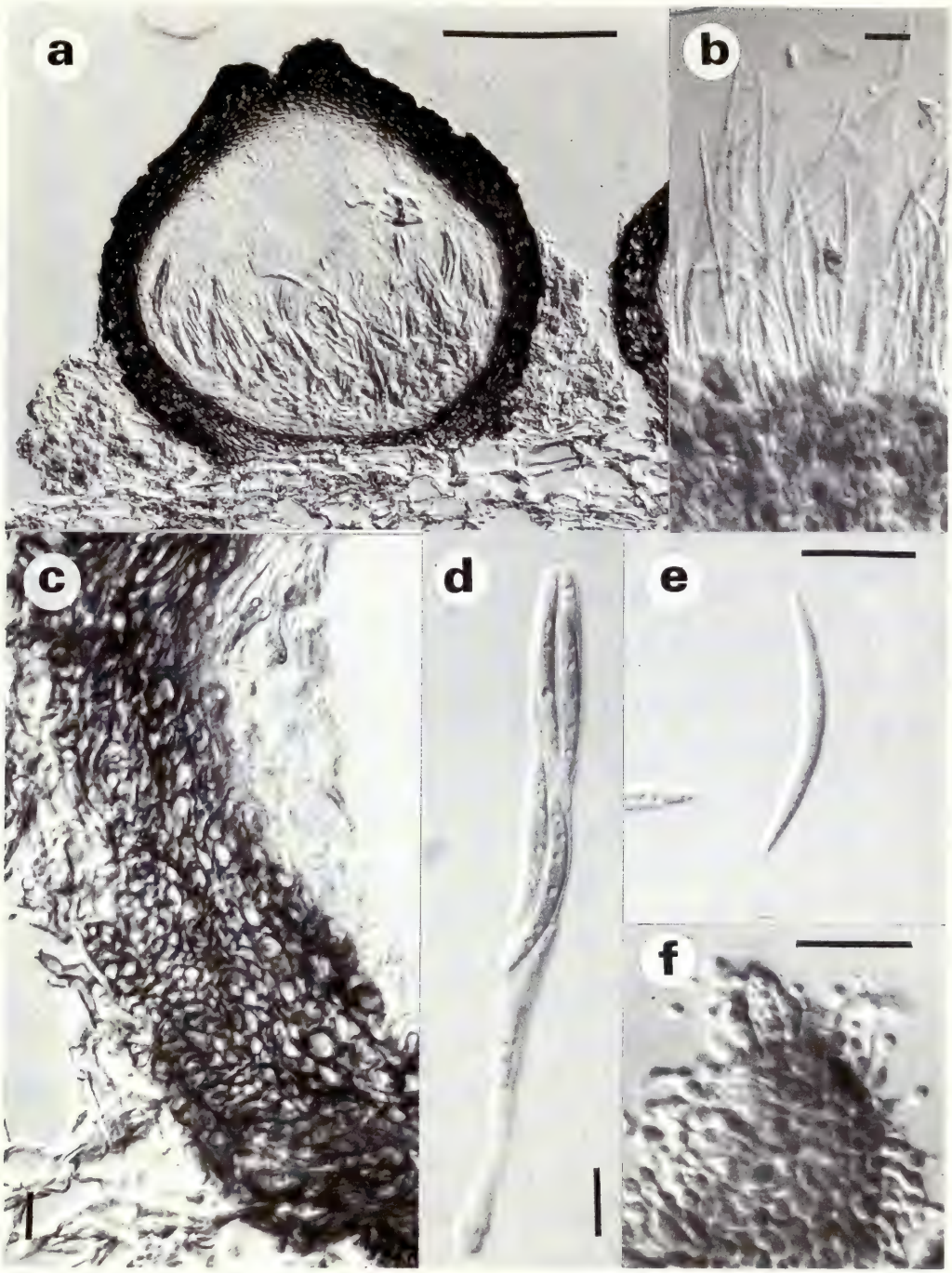


Fig. 49 *Cresporhaphis wienkampii* (Lahm ex Hazslin) Aguirre (BM–isoneotype) (a) Vertical section of ascoma showing chlorococcoid algae at the sides; scale = 100 μm; (b) Paraphyses; (c) Detail of exciple: textura angularis; (d) Ascus and ascospores; (e) Ascospore; (f) Conidiogenous cells and conidia; scale = 10 μm.

TYPIFICATION. Type material of *Cresporhaphis wienkampii* collected previous to the date of publication of the new taxon was not located in Lahm's herbarium (B). Nevertheless the material was widely collected and also several exsiccata of the species were distributed. Since earlier material of the species was not located, a specimen from Rabenhorst, *Lich. europ. exs.* no. 651 (1862) at L is here selected as the neotype, since the material was collected by Wienkamp on bark of *Salix fragilis*, and it is in very good condition with abundant ascomata.

OBSERVATIONS. The species does not present the host specificity common in the other species described in the genus. It differs from *C. acerina* and *C. muelleri* also with aseptate ascospores, primarily in its broader ascospores and the lack of a distinct apical cap. Also it differs from *C. acerina* in the

bluish iodine reaction of the hymenial gelatin and in the presence of numerous ascomata. *C. muelleri* presents, like *C. wienkampii*, a coloured iodine reaction, but in the former the ascomata are mainly confluent.

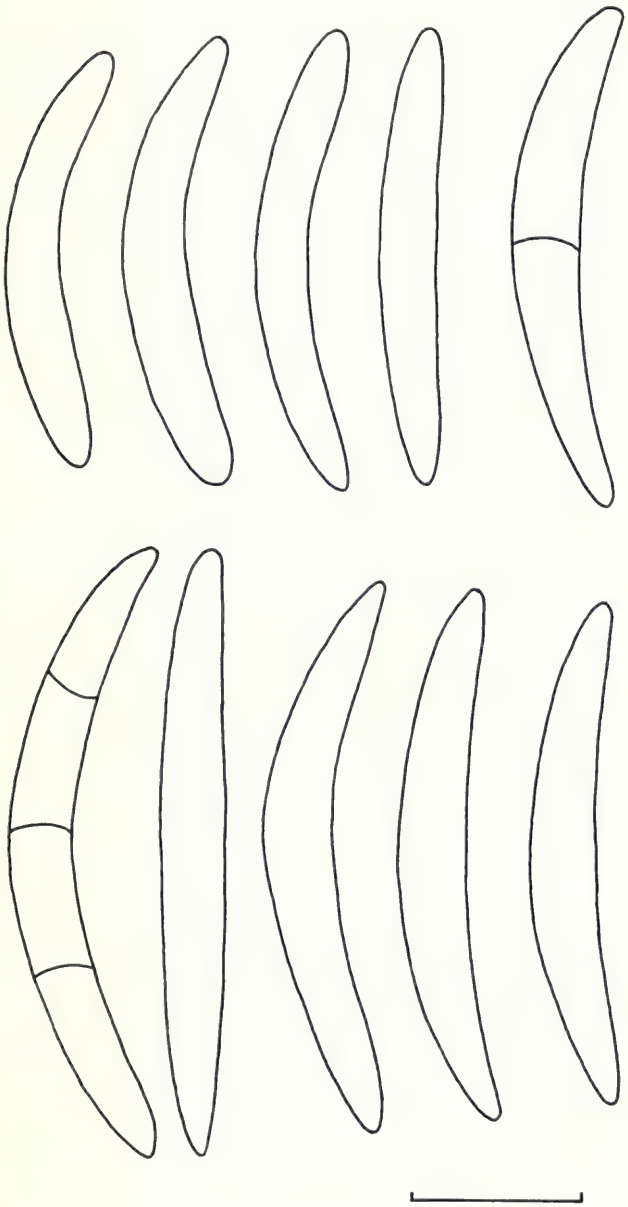


Fig. 50 Ascospore outlines of *Cresporhaphis wienkampii* (Lahm ex Hazslin) Aguirre (B 44683, W 11811); scale = 10 μm.

ADDITIONAL SPECIMENS. **Czechoslovakia**, Bohemia, '... [illegible] Brad', 1888, *L. Nowakowski* (WRSL). Presov ['Eperies'], ad 'Salices vetustas', 1863, *F.A. Hazslinsky* [Körber, *Lich. Sel. Germ.* exs. no. 263, as *Leptorhaphis wienkampii*] (BM, W 19923, 11811); loc. cit. (BM, W 21989). **Germany**, Westfalen, Münster, Handorf, January 1862, *P. Wienkamp* (L, L 33, B 44683, BM); loc. cit., *J. G. F. X. Lahm* (W); loc. cit., on *Salix fragilis*, *T. R. J. Nitschke* (W, BM); loc. cit., on *Salix*, *J. G. F. X. Lahm* (B 59589). Lutkenbeck, August 1860, *T. R. J. Nitschke* (B 59621); loc. cit., on *Ulmus*, August 1867, *J. G. F. X. Lahm* (B 59588). Wellbergen, August 1862, *J. G. F. X. Lahm* (B 59587). **Norway**, 'Saem, Snaasm paroch.', J. M. Norman (O). Trondheim ['Trondhjem'], on *Populus*, July 1863 (BM). **Poland**, Katowice, Rybnik, Parusihowitz, on *Salix*, August 1872, *B. Stein* (B 59693). **Sweden**, '*Salix*' (BM-ACH 311, as *Verrucaria byssacea* var. *stictica* Ach.). Närke, *P. B. Hellbom* (BM–3 specimens). [Sine loco], on *Salix babylonica*, *B. Everken* (WRSL 29)., [Sine. loc.], on *Salix* (B 59632).

V. **Rhaphidicyrtis** Vainio

Rhaphidicyrtis Vainio in *Acta Soc. Fauna Flora fenn.* **49**(2): 216 (1921). Type species: *Rhaphidicyrtis trichosporella* (Nyl.) Vainio [syn. *Mycoporum trichosporellum* Nyl.] (holotype).

Thallus: Crustose, smooth to pulverulent, creamy-white to grey, continuous, not delimited by a prothallus; epiphloeodal to endophloeodal, associated with trentepohlioid algae.

Ascomata: Perithecioid, black, smooth, more or less immersed in the substratum, globose and ostiolate. Involucrellum: dark brown, covering the ascomata, clypeate, not changing colour in 10% KOH. Exciple: continuous, dark brown, becoming colourless towards the centrum; consisting of a pseudoparenchymatous tissue of isodiametric and mesodermatous cells, radially compressed, becoming a textura porrecta in places. Hamathecium: of colourless paraphysoids enveloped in mucus, and also colourless periphyses in the ostiolar canal; hymenial gelatin deep blue in iodine. Asci: arising from the base of the ascomatal cavity, ripening sequentially, cylindrical, short-stalked, with two distinct wall layers, the outer thin and smooth, the inner thicker at the apex, without an internal apical beak, not changing colour in iodine; 8-spored; discharge not observed. Ascospores: arranged in a fascicle within the ascus, sometimes helically twisted, colourless, thin-walled, smooth, very long and filiform to somewhat sigmoid, multiseptate, without appendages or gelatinous sheaths.

Conidiomata: Not observed.

RELATIONSHIPS. The genus *Rhaphidicyrtis* Vainio (1921) was erected to accommodate the single species *Mycoporum trichosporellum* Nyl. This taxon has subsequently been referred to different genera and was included in *Leptorhaphis* by Riedl (1962, 1963), on the basis of the ascospore morphology. Although I concur with Riedl's objections to Vainio's referral of the genus to the Microthyriaceae, as it lacks strongly flattened thyriothecioid ascoma, formed of plates of radially oriented cells, and further possesses paraphysoids and periphyses, it is neither referable to the genus *Leptorhaphis* nor indeed to the family Arthopyreniaceae. Furthermore, the ascomatal structure is reminiscent of the perithecia of developed ascomata of *Porina byssophila* (Nyl.) Arnold, discussed by Janex- Favre (1981: 268), also consisting of a subglobose cavity formed by a secondary wall, which I called exciple, covered by an involucrellum. The genus *Rhaphidicyrtis* is consequently accepted here as a separate genus, which must be placed in the Pyrenulales on the basis of the hamathecial and ascus structure, but no appropriate family has been found to accommodate it satisfactorily.

The species

1. **Rhaphidicyrtis trichosporella** (Nyl.) Vainio in *Acta Soc. Fauna Flora fenn.* **49**(2): 217 (1921). *Mycoporum*

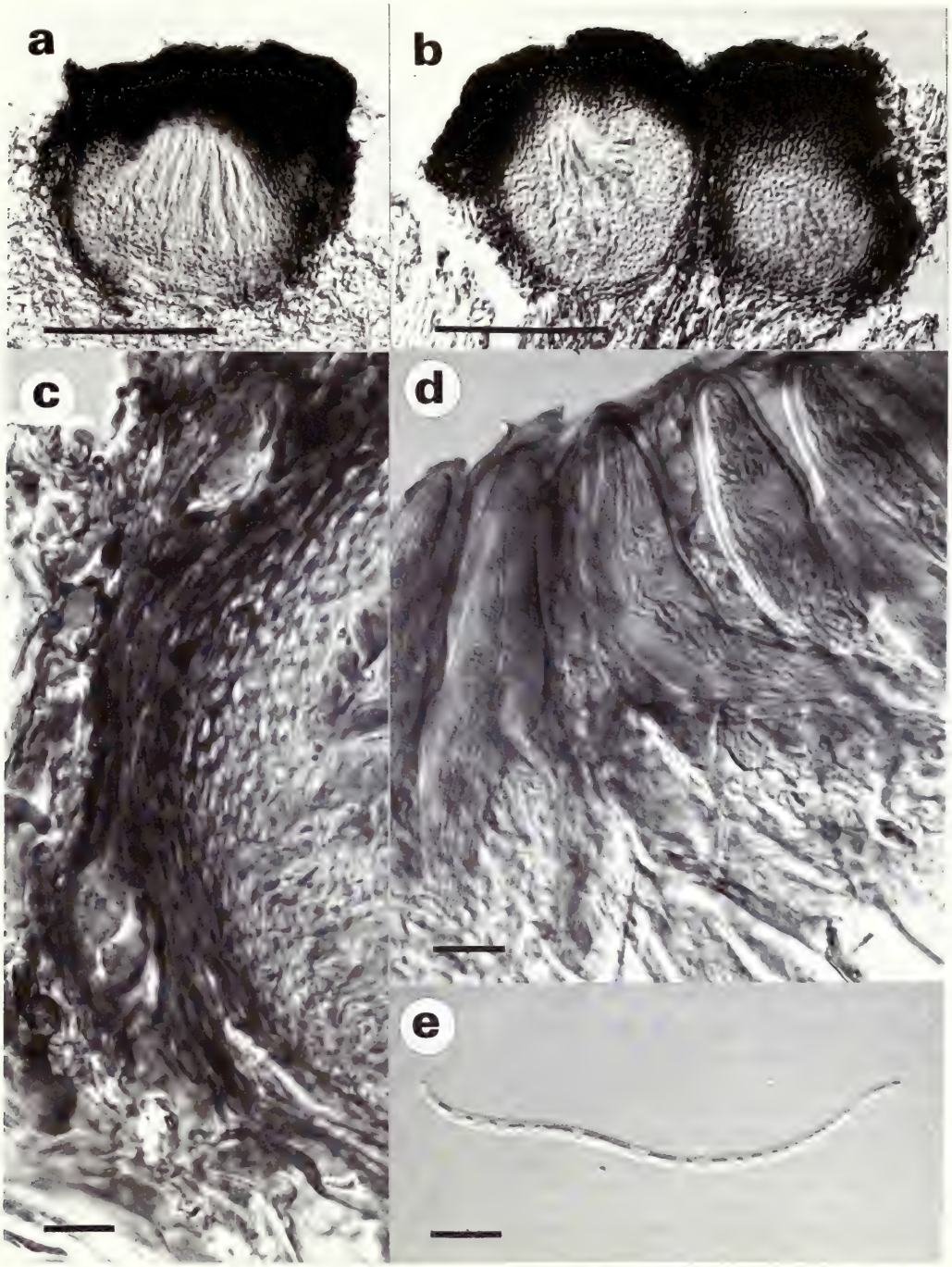


Fig. 51 *Raphidicyrtis trichosporella* (Nyl.) Vainio (H-NYL 4285–holotype of *Mycoporum trichosporellum*) (a) Vertical section of ascoma; scale = 100 μm; (d) Asci and ascospores, hymenial gelatin showing deep blue iodine reaction; (e) Ascospore; scale = 10 μm; B 44684–holotype of *Leptorhaphis wolbecensis* (b) Vertical section of ascomata; scale = 100 μm; (c) Detail of exciple: textura angularis to porrecta; scale = 10 μm.

trichosporellum Nyl. in *Flora, Jena* **57**: 14 (1874). *Mycoporellum trichosporellum* (Nyl.) Zahlbr. *in* Engler & Prantl, *Nat. Pflanzenfam.* **1**(1): 78 (1907). *Leptorhaphis trichosporella* (Nyl.) Riedl in *Sydowia* **16**: 228 (1963). Type: Finland, Fennia, Tavastia australis, Padasjoki: Nyystölä, 'ad corticem Betulae', 1872, *E. Lang* (H-NYL 4285!—holotype, TUR-VAINIO 32714!—isotype).

Leptorhaphis wolbecensis Lahm in *Jber. westf. Prov. Ver. Wiss. kunst* **13**: 73 (1885). Type: Germany, Westfalia, near Münster, Wolbeck Tiergarten, on *Carpinus*, February 1863, *T. Nitschke* (B 44684!—holotype).

Fig. 51, 52.

Thallus: Smooth to pulverulent in places, creamy-white to grey, continuous, not well delimited; superficial to immersed in the bark, composed of colourless to pale brown, thin-walled

and smooth hyphae, less than 3 μm broad, with numerous septa and constricted at them; associated with trentepohlioid algae, filaments *c.* 6 μm wide.

Ascomata: Perithecioid, black, smooth, numerous, individually scattered, *c.* 150–200 μm diam; immersed to half-immersed in the substratum, globose, with a centrally located ostiole, which is slightly depressed. Involucrellum: dark brown layer, *c.* 30 μm thick, becoming thicker, *c.* 60 μm, and darker near the ostiole, clypeate, composed of bark material and dark brown, thin-walled, smooth hyphae. Exciple: continuous wall, dark brown, becoming colourless internally, 15–30 μm thick; composed of dark brown, thick-walled, smooth hyphae, less than 3 μm wide, forming a pseudoparenchymatic tissue of isodiametric and mesodermatous cells, with dark brown and thick walls, *c.* 5 μm diam, radially compressed, becoming a textura porrecta in places. Hamathecium: of paraphysoids, composed of colourless, smooth, branched and anastomosing, thin-walled hyphae, 1.5–2 μm wide, with infrequent septa, enveloped in mucus; periphyses lining the ostiolar canal, colourless, smooth, thin-walled, less than 2 μm wide; hymenial gelatin deep blue in iodine. Asci: cylindrical, short-stalked, 75–95 × 9–15 μm; with two distinct wall layers, the outer thin and smooth, the inner thicker at the apex, without an internal apical beak, not changing colour in iodine; 8-spored. Ascospores: arranged in a fascicle within the ascus, sometimes helically twisted, colourless, thin-walled, smooth, filiform to somewhat sigmoid, (60–) 75–95 × 2–3 μm, 7-, 9- or more septate, not constricted at the septa, attenuated at the apices.

Conidiomata: Not observed.

ECOLOGY. On smooth bark of *Betula* spp., *Carpinus betulus* L., *Ilex aquifolium* L. and *Quercus robur* L., growing with other lichenized fungi such as *Thelotrema lepadinum* (Ach.) Ach., *Pachyphiale carneola* (Ach.) Arnold, or *Phlyctis argena* (Sprengel) Flotow, in old deciduous woodlands of temperate regions; not causing any apparent damage; lichenized, with a trentepohlioid photobiont.

DISTRIBUTION. Known only from Finland, Germany, and the British Isles. Not previously recognized as a British species.

TYPIFICATION. I agree with Riedl (1963: 230) that the holotype of *Mycoporum trichosporellum* must be the single specimen in Nylander's Herbarium in H; another collection from TUR is an isotype. Only one specimen, kept at B, fulfils the characteristics given in the protologue for *Leptorhaphis wolbecensis*, and is consequently taken as being the holotype for that name.

OBSERVATIONS. On occasions *Rhaphidicyrtis trichosporella* has been mistaken for *Celothelium ischnobelum* (Nyl.) Aguirre. Both species have very long and filiform ascospores, but differ in the ascomatal structure. Thus the ascomata are always solitary in *R. trichosporella*, whereas several ascomata are covered by a common involucrellum in *C. ischnobelum*. Also, the ascus apex is not capped by a meniscus in *R. trichosporella*, and this species shows a clear blue iodine reaction of the hamathecial gelatin.

ADDITIONAL SPECIMENS. **British Isles**, Scotland, Westerness, Glen Cripesdale, on *Ilex*, August 1970, *F. Rose* (BM). Easterness, Nairn, Cawdor Wood, on *Ilex*, 25 August 1986, *B. J. Coppins* 11502 (E). Flora of West Ross, Valley of Abheinn near Fuirneis, Loch Maree, Letterewe Woods, 1 km SE. of Letterewe House, on *Ilex*, 23 June 1986, *B. J. Coppins* & R.G. Woods 11861 (E). Eire, Wicklow, SE. of Lough Dam, on *Betula*, in damp part of oak and birch wood, 4 April 1976, *B. J. Coppins, C. J. B. Hitch & M. R. D. Seaward* 1648 (E). **Germany**, Westfalia, *J. G. F. X. Lahm* (L). Oldenburg, Zwischenahn, forest near Helle, 'an mittelgrossen Eichen', January 1890, *H. Sandstede* [Arnold, *Lich. exs.* no. 1510, as *Leptorhaphis quercus*] (PAD, PC-HUE 3505/3). Oldenburg, near Yever, Forste Upjever, on *Betula*, November 1886, *H. Sandstede* [Zwackh, *Lich. exs.* no. 1060, as *Verrucaria quercus*] (PC-HUE 3505/3, B 59722).

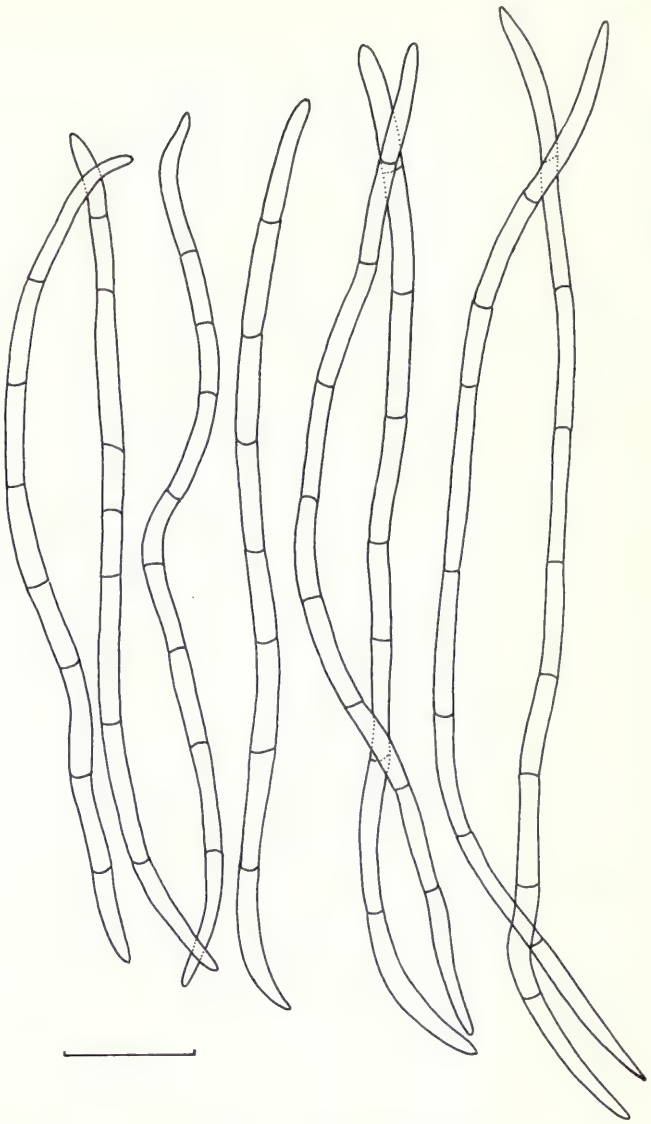


Fig. 52 Ascospore outlines of *Rhaphidicyrtis trichosporella* (Nyl.) Vainio (H–NYL 4285–holotype of *Mycoporum trichosporellum*); scale = 10 μm.

VI. **Sarcopyrenia** Nyl.

Sarcopyrenia Nyl. in *Mém. Soc. Acad. Angers* **4**: 69 (1858). Type species: *Verrucaria gibba* Nyl. [*Sarcopyrenia gibba* (Nyl.) Nyl.] (holotype)

Lithosphaeria Beckh. *in* Körber *Parerg. lich.*: 344 (1863). Type species: *Lithosphaeria geisleri* Beckh. (holotype).

Sarcopyreniomyces Cif. & Tom. in *Atti Ist. bot. Univ. Lab. Crittog. Pavia* V, **10**: 36, 59 (1953). Type species: *Sarcopyrenia gibba* (Nyl.) Nyl. (holotype); nom. illeg. (Arts 13.1(d), 63.1).

Thallus: When present, olivaceous-grey, squamulose-granulose, not well delimited, associated with a green photobiont; presumably belonging to more or less deteriorated crustose lichens.

Ascomata: Perithecioid, conical to subglobose, carbonaceous, black and brittle, verrucose, scattered singly; half-immersed to superficial, with a central ostiole located in a papilla. Wall: continuous, not changing colour in KOH, composed of three layers, each forming a textura angularis: the outer always carbonaceous, consisting of isodiametric, thick-walled cells, with enlarged lumina and black walls only observed with SEM; the middle wall, colourless to blackish, consisting of isodiametric, thin- walled cells, with enlarged lumen and greenish-black to black walls, usually bigger than those of the outer wall; the inner wall, thinner, hyaline to blackish, composed of smaller not isodiametric cells, becoming laterally compressed, with thin, colourless to blackish walls and enlarged lumen. Hamathecium: of paraphyses, soon becoming evanescent; periphyses present in the ostiole; hymenial gelatin not changing colour in iodine. Asci: arising from the base and angles of the ascoma cavity, ripening synchronously, cylindrical, short-stalked, unitunicate in structure, thin-walled, thicker towards the apex, becoming evanescent, not changing colour in iodine; apical structures not observed; 8-spored; asci presumably open through deliquescence of the ascus wall. Ascospores: biseriately arranged in the asci, colourless, thin-walled, filiform, sometimes sigmoid, with somewhat capitate apices, 0-, 1-septate, not constricted at the septa, without appendages or gelatinous sheaths.

Conidiomata: Not observed.

NUMBER OF SPECIES. Three species are accepted here, distinguished primarily on the basis of ascospore morphology, size and septation. However, during the preparation of this manuscript, Navarro-Rosinés & Hladún (1990) described a new species *Sarcopyrenia bacillospora* Nav., Ros. & Hladún from Catalunya (Spain), also on limestones, with aseptate and smaller spore size than the species treated in the present work. They also recognized a new variety: *Sarcopyrenia gibba* var. *geisleri* Nav., Ros. & Hladún, and possibly another new species from the south of Spain (Almería Province), although this was left undescribed due to the lack of sufficient material.

ECOLOGY. Lichenicolous on crustose lichenized fungi growing on siliceous and calcareous rocks (Navarro-Rosinés & Hladún, 1990).

DISTRIBUTION. Reported from the Northern Hemisphere in temperate and mediterranean regions of Europe and northern Africa (Poelt, 1969; Clauzade & Roux, 1985; Navarro-Rosinés & Hladún, 1990).

TYPIFICATION. Since first described by Nylander (1858: 69), most lichenologists regarded *Sarcopyrenia* as a monotypic genus, including only *Sarcopyrenia gibba* (Nyl.) Nyl., as holotype species. Keissler (1938: 265) referred a second species to the genus: *Leptorhaphis beckhausiana* Lahm [i.e *Sarcopyrenia beckhausiana* (Lahm) Aguirre, Nav.,Ros. & Hladún], but he failed to validate the new combination, and this has been overlooked. He also regarded *Lithosphaeria geisleri* Beckh. as a synonym of *S. gibba*, and (since the former is the holotype of the genus *Lithosphaeria* Beckh., also monotypic, both genera are regarded as synonymous. I have not seen holotype material of *L. geisleri* from Körber's herbarium at L; however, Beckhaus' description of the species in Körber (1865: 345), and the study of authentic material of this taxon from Höxter (Westfalia, West Germany) kept in BM, presumably an isotype, supports Keissler's opinion.

Farr et al. (1979) and Eriksson & Hawksworth (1987*c*) included another generic name as a synonym of *Sarcopyrenia*: *Sarcopyreniopsis* Cif. & Tom. (1953). However, Ciferri & Tomaselli (1953: 36, 59-60) only referred to the genus *Sarcopyreniomyces* in their article, and since I was unable to locate the former generic name, this was excluded from the list of synonymy. *Sarcopyreniomyces* is a su erfluous name for *Sarcopyrenia*, since both genera are based on the same type species.

RELATIONSHIPS. On the basis of major generic features such as ascomata structure and the presence of paraphyses and periphysate ostioles, as well as in its saxicolous habitat, *Sarcopyrenia* has been traditionally regarded as a member of the Verrucariales. Thus Eriksson & Hawksworth (1987*b*) included the genus tentatively within the single family of the order, the Verrucariaceae Eschw. According to Janex-Favre (1970) and Henssen & Jahns (1974) the asci of the Verrucariaceae are regarded as functionally 'bitunicate' with fissitunicate dehiscence. This was also accepted by Eriksson (1981: 169) after studying the mechanism of discharge and ascus structure of *Verrucaria rupestris* Schrader. He also suggested that similar types of ascomata are found within the Nectriaceae, but in these the asci are not bitunicate. Studies of dried herbarium material of *Sarcopyrenia* showed that the ascus wall is thin and evanescent, probably releasing the spores passively, and resemble the ascus structure of some nectriaceous fungi (Rossman, 1983: 7). The latter also described the centrum of the hypocrealean fungi as having pseudoparaphysis-type interthecial filaments, becoming evanescent and gelatinous among the asci, with periphyses in the ostiole, and always lacking true paraphyses. However, *Sarcopyrenia* is here described as having paraphyses, soon becoming evanescent.

Sarcopyrenia also shows certain similarities in ascomal structure to the lichenicolous genera *Lasiosphaeriopsis* D. Hawksw. & Sivanesan (in Hawksworth, 1980: 371; Eriksson & Santesson, 1986) and the monotypic *Rhagadostoma* Körber. Both genera have been referred to the Nitschkeaceae, and the cells of the ascomatal wall have very distinct Munk pores. However, these pores were not observed in *Sarcopyrenia*. Consequently the systematic position of this genus remains uncertain, but obviously requires a new emplacement other than in the Verrucariales.

Key to the species

1. Ascospores 0-septate 2
– Ascospores 1-septate ..... 2. **S. cylindrospora**

2(1). Ascospores filiform, apices rounded, never capitate ..... 1. **S. beckhausiana**
– Ascospores cylindrical-sigmoid, apices capitate ..... 3. **S. gibba**

The species

1. **Sarcopyrenia beckhausiana** (Lahm) Aguirre, Nav., Ros. & Hladún *in* Navarro-Rosinés & Hladún in *Candollea* **45**:

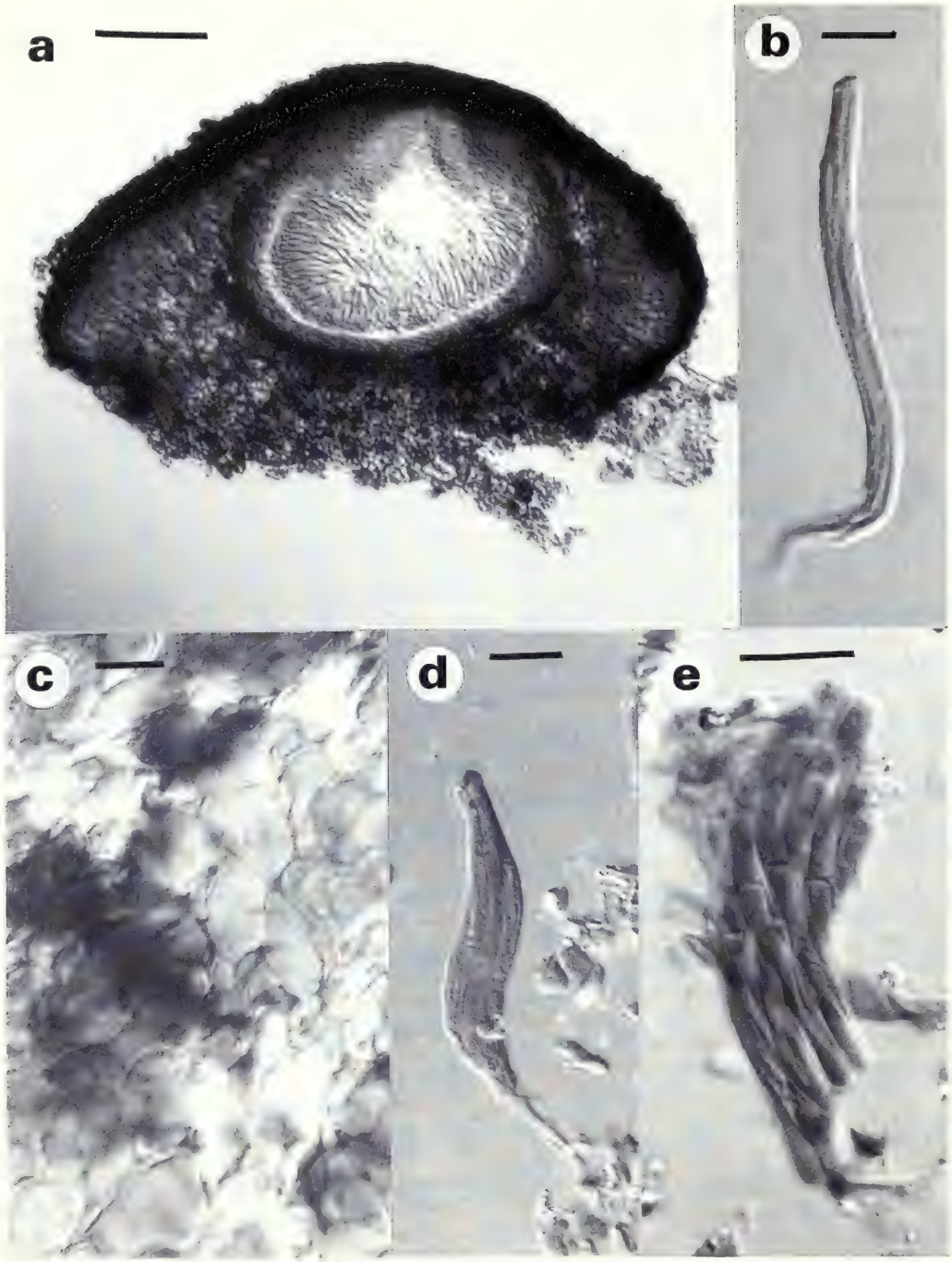


Fig. 53 *Sarcopyrenia beckhausiana* (Lahm) Aguirre, Nav., Ros. & Hladún (B 44881–lectotype) (a) Vertical section of ascoma; scale = 100 µm; (b) Ascus and ascospores; scale = 10 µm. *Sarcopyrenia cyclindrospora* (P. Crouan & H. Crouan) Aguirre (Concarneau–holotype) (c) Detail of ascus wall: textura globulosa-angularis; (d) Ascus and ascospores, ascus wall very faint; (e) Ascospores; scale = 10 µm.

472 (1990). *Leptorhaphis beckhausiana* Lahm, in Körber *Parerg. lich.*, 386 (1865). *Sarcopyrenia beckhausiana* (Lahm) Keissler, *Rabenh. Krypt.,Fl.* **9**, 1(2): 265 (1938); nom. inval. (Art.33.1). Type: Germany, Nordrhein-Westfalen, Brunsberg, Höxter, on limestone, March 1864, *K. Beckhaus* (B 44881!—lectotype, selected here; L!—isolectotype, immature).

Fig. 53, 54B.

Thallus: Not observed.

Ascomata: Perithecioid, subspherical to applanate, carbonaceous, brittle, shiny, verrucose scattered singly, 0.5–1.2 mm diam; superficial, with a central ostiole located in a papilla. Wall: continuous, composed of three layers forming a

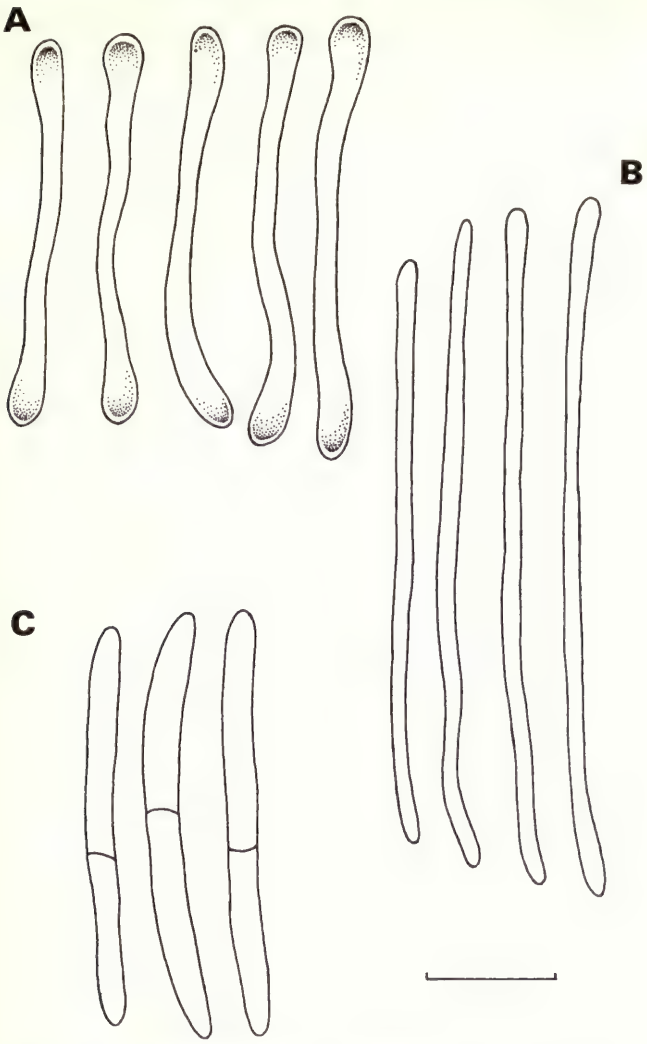


Fig. 54 Ascospore outlines (A) *Sarcopyrenia gibba* (Nyl.) Nyl. (H–NYL 4058–holotype); (B) *Sarcopyrenia beckhausiana* (Lahm) Aguirre, Nav., Ros. & Hladún (B 4488–lectotype); (C) *Sarcopyrenia cylindrospora* (P. Crouan & H. Crouan) Aguirre (Concarneau–holotype); scale = 10 μm.

textura angularis: the outer completely carbonaceous, *c.* 25–40 μm thick, consisting of isodiametric, thick-walled cells, *c.* 4–7.5 μm; the middle wall is colourless to blackish, thicker at the bases of the ascomata, composed of isodiametric, thin-walled cells, 6–15 μm diam, with enlarged lumen and blackish walls; the inner wall is thinner again, 35–40 μm thick, colourless to blackish, becoming darker towards the middle wall, composed of thin-walled cells, not isodiametric, laterally compressed, and narrower and smaller than those from the outer and middle walls, *c.* 4 μm wide, with colourless to blackish walls and enlarged lumina. Hamathecium: paraphyses not observed; periphyses composed of colourless, unbranched hyphae, less than 2 μm thick; infrequently septate, not constricted at the septa, with a slightly capitated apical cell. Asci: arising from the base and angles of the ascoma cavity, numerous, cylindrical, short-stalked, one-layered, 60–70 × 4–6.5 μm, thin-walled; 8-spored; opened asci not observed, but ascus wall probably evanescent. Ascospores: biseriately arranged in the asci, colourless, smooth, thin-walled, filiform, 50–60 × (1.5–) 2–2.5 μm, with rounded apices, aseptate.

ECOLOGY. On crustose lichen thalli found on calcerous rocks.

DISTRIBUTION. Europe, known from the type locality in Germany, and recently collected in Catalunya (Spain) by P. Navarro-Rosinés & Hladún (1990), although material of the latter was not studied.

TYPIFICATION. Only two type collections of this taxon were located at L and B. The material from Körber's 'typenherbar' at L is immature, and the specimen in B is consequently selected here as the lectotype.

OBSERVATIONS. Keissler (1938: 265) suggested that this species should be referred to *Sarcopyrenia* on the basis of the ascomatal structure and ascus morphology, and associated the epithet '*beckhausiana*' in the packet found in B herbarium; however, he failed to validate the new combination.

S. beckhausiana differs from *S. gibba*, also with aseptate ascospores, in having filiform instead of sigmoid ascospores, and with only slightly capitate apices.

2. **Sarcopyrenia cylindrospora** (P. Crouan & H. Crouan) Aguirre *in* Navarro-Rosinés & Hladún in *Candollea* **45**: 476 (1990). *Verrucaria cylindrospora* P. Crouan & H. Crouan, *Fl. Finist.*: 86 (1867). *Leptorhaphis cylindrospora* (P. Crouan & H. Crouan) Boistel, *Nouv. Fl. Lich.* **2**: 287 (1903). Type: France, Brittany, Finistère, 'sur les rochers de gneiss', October 1866, *P. L. & H. M. Crouan* (Concarneau!—holotype).

Fig. 53B, 54C.

Thallus: Presumably belonging to deteriorated crustose lichenized fungi; yellowish, squamulose to granulose, not continuous and not well delimited; superficial, composed of colourless hyphae, *c.* 2 μm wide, septate, not constricted at the septa, associated with globose chlorococcoid algae.

Ascomata: Perithecioid, subspherical to applanate, carbonaceous, brittle, shiny, verrucose, scattered singly, 400–600 μm diam; half immersed in the thallus, with a central ostiole located in a papilla. Wall: continuous, composed of three layers: the outer thin and very dark, almost black; the middle layer thicker, *c.* 70–100 μm thick, colourless, becoming black towards the sides and tip of the ascomata, composed of isodiametric thin-walled cells, 7.5–15.5 μm diam, with enlarged lumina and blackish walls, forming a textura angularis to globulosa; the inner wall thinner, *c.* 30 μm thick, colourless, becoming darker towards the outer wall, composed of thin-walled cells, not isodiametric, laterally compressed, smaller than those of the outer wall, less than 5 μm wide, with enlarged lumina and colourless to dark walls, forming a textura angularis. Hamathecium: paraphyses not observed; periphyses, colourless, unbranched, broad hyphae, less than 2 μm thick, infrequently septate. Asci: cylindrical-clavate, short-stalked, apparently 'unitunicate', 45–55 μm × 5–6.5 μm, thin-walled at the sides, becoming only thicker at the apex; '8-spored. Ascospores: biseriately arranged in the asci, colourless, smooth, thin-walled, filiform to sigmoid, 35–40 × 2–3 μm, with rounded apices, 1-septate, not constricted at the septa.

ECOLOGY. The species was described as growing on gneiss. However, a recent collection from Catalunya (Spain) was found to be parasitic on a thallus of *Aspicilia* cf. *contorta* (Navarro-Rosinés & Hladún, 1990).

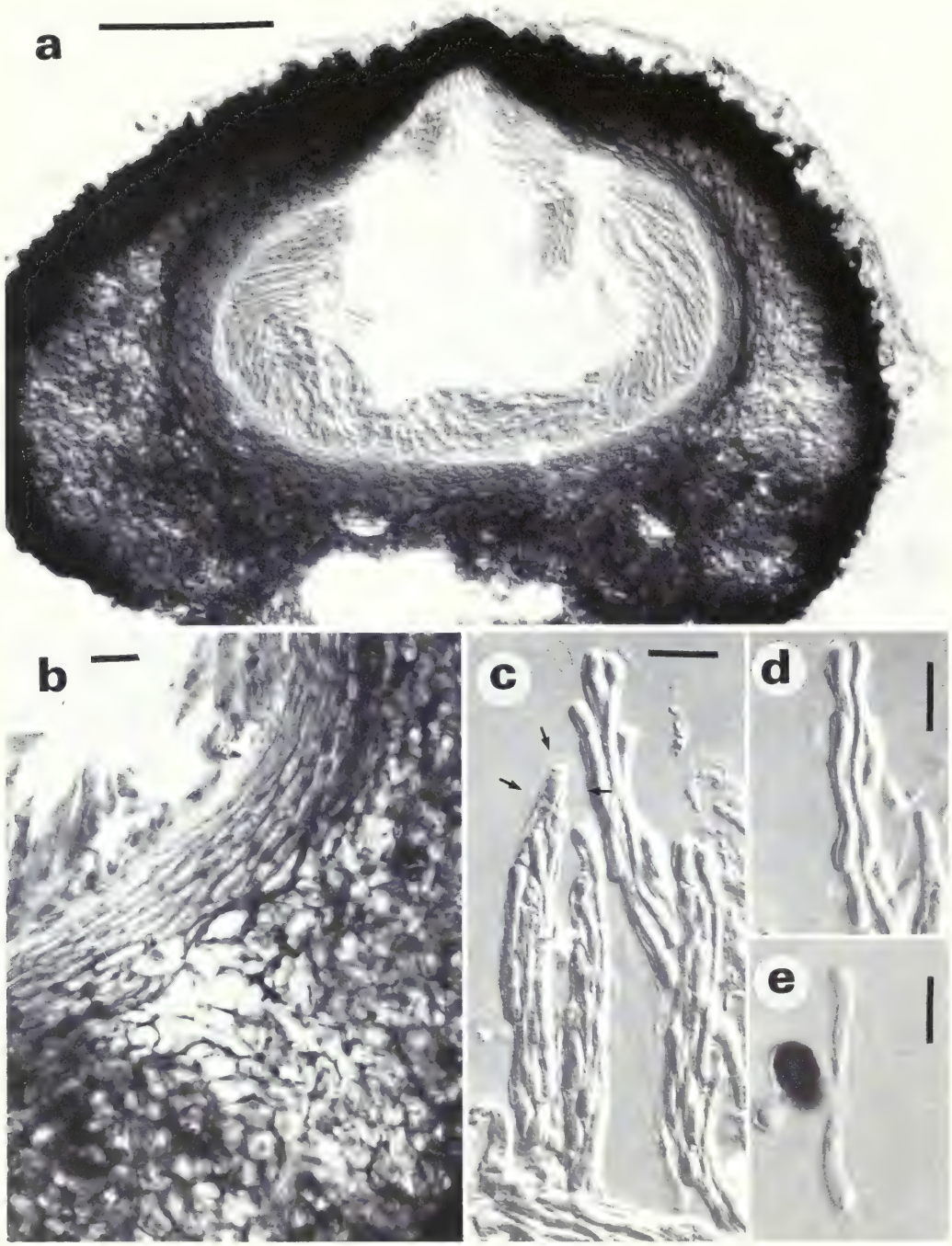


Fig. 55 *Sarcopyrenia gibba* (Nyl.) Nyl. (H–NYL 4058–lectotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of wall layers: textura angularis and textura somewhat prismatica, with cells compressed laterally; (c) Ascus and ascospores, arrows showing faint ascus wall; (d), (e) Ascospores; scale = 10 μm.

DISTRIBUTION. Europe, known from the type locality (France) and from a recent collection in Catalunya (Spain); material of the latter was not studied.

OBSERVATIONS. This species is represented in the Crouan Herbarium in Concarneau by one specimen in very poor condition, with only one ascoma left in the packet. Therefore Keissler (1938: 265) suggested that the taxon should be excluded as a fragile species. Nevertheless the species is easily recognizable as a member of the genus *Sarcopyrenia*, differing from *S. gibba* and *S. beckhausiana* in its septate ascospores. If new material of the species is found it would be convenient to select a neotype, for there is only very little material of the holotype left.

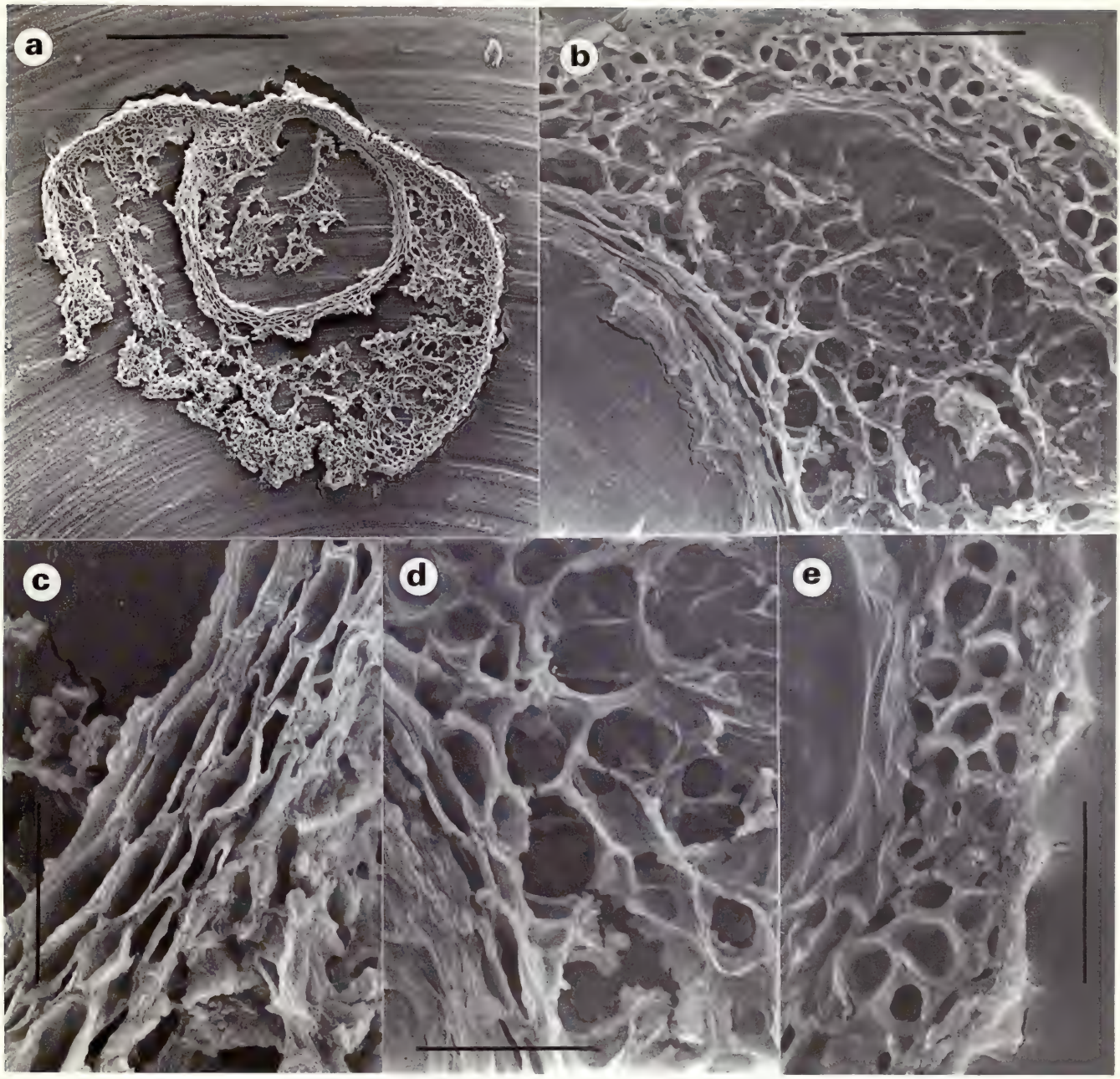


Fig. 56 *Sarcopyrenia gibba* (Nyl.) Nyl. (H–NYL 4058–lectotype) (a) Vertical section of ascoma; scale = 200 μm; (b) Detail of exciple: 3-layered wall, textura angularis; scale = 43 μm; (c) Detail of inner layer: textura angularis with laterally compressed cells; scale = 17.6 μm; (d) Detail of middle layer: textura angularis; scale = 20 μm; (e) Detail of outer layer: textura angularis; scale = 20 μm.

3. **Sarcopyrenia gibba** (Nyl.) Nyl. in *Mém. Soc. Impér. Sci. nat. Cherbourg* **5**: 337 (1857). *Verrucaria gibba* Nyl. in *Mém. Soc. Impér. Sci. nat. Cherbourg* **2**: 342 (1854). *Leptorhaphis gibba* (Nyl.) Boistel, *Nouv. Fl. Lich.* **2**: 287 (1903). Type: Algeria, Constantine, 'ad saxa calcerea (Balansa)' (H-NYL 4058!—lectotype, selected here; NYL 4057! & 7522!—isolectotypes).

Lithosphaeria geisleri ['Geisleri'] Beckh. *in* Körber, *Parerg. lich.*: 345 (1863). Type: West Germany, Wesfalia, Höxter, ' . . . [illegible] suspicor fungillum in crusta lichenis . . . [illegible] parasiti . . . tem c. Lahm', *K. Beckhaus* (BM!—isotype).

Verrucaria armorica P. Crouan & H. Crouan, *Fl. Finist.*: 86, 256 (1867). *Leptorhaphis armorica* (P. Crouan & H. Crouan) Boistel, *Nouv. Fl. Lich.* **2**: 287 (1903). Type: France, Brittany, Finistère, 'sur les roches de gneiss, a l'ombre, douves des fortifications', 24 October 1866, *P. L. & H. M. Crouan* (Concarneau!—holotype).

Fig. 54A, 55, 56.

Thallus: Olivaceous-green, becoming yellowish ochre when dry, matt, granulose to squamose, superficial, not continuous, not well delimited; associated with globose chlorococcoid algae; presumably belonging to crustose lichenized fungi.

Ascomata: Perithecioid, subspherical to applanate, carbonaceous, verrucose, scattered singly, sometimes confluent, 0.5–1 mm diam; superficial, with a central ostiole located in a papilla. Wall: continuous, composed of three layers: the outer completely carbonaceous, *c.* 25–35 µm; the middle layer, blackish and thicker at the base of the ascoma, *c.* 90 µm thick, composed of isodiametric, thin-walled cells, 4–10 µm diam, with enlarged lumina and blackish walls, forming a *textura* angularis to globulosa; the inner wall much thinner, *c.* 20 µm, colourless, becoming darker towards the outer wall; composed of thin-walled cells not isodiametric, laterally compressed, with colourless to blackish walls, smaller than those of the outer and middle layers, forming a textura angularis. Hamathecium: of paraphyses, composed of colourless smooth thin-walled cells, less than 1.75 µm wide, with infrequent septa, occasionally branching, enveloped in mucus, scarcely staining in lactophenol cotton-blue, becoming evanescent; periphyses composed of colourless, unbranched hyphae, less than 2 µm thick, infrequently septate, not constricted at the septa and with rounded last cell. Asci: cylindrical, short-stalked, one- layered, 55–70 × 7–9.5 µm, smooth, thin-walled at the sides, thickening towards the apex; no other apical structures seen; 8-spored; opened asci not observed, ascus wall evanescent. Ascospores: biseriately arranged in the asci, sometimes helically twisted, colourless, smooth, thin-walled, sigmoid, 25–35 (–45) × 3–4.5 µm, with capitate apices, 0-septate.

ECOLOGY. Crouan & Crouan (1867: 256) described *Verrucaria armorica* as growing on gneiss, and having no thallus. Studies of type material of the species prove that this taxon is synonymous with *Sarcopyrenia gibba* Nyl., a lichenicolous fungus usually growing on crustose lichens found in basic rocks or limestone. In the British Isles it has recently been recorded in several churchyards in Somerset, Derbyshire, and Lincolnshire, on marble, magnesium limestone and oolite respectively (Hitch & Cayton, 1986: 32).

DISTRIBUTION. Known from the British Isles (Cannon et al., 1985; Hitch & Cayton, 1986), central and southern Europe (Clauzade & Roux, 1985; Navarro-Rosinés & Hladún, 1990), and Algeria; with scattered distribution.

TYPIFICATION. *Verrucaria armorica* presented no problem for typification since only one specimen which agreed with the protologue was found in the Crouan herbarium in Concarneau. H-NYL 4058 is selected as lectotype of *Sarcopyrenia gibba* since it is in better condition than other isotype specimens in Nylander's herbarium. Finally, type material of *Lithosphaeria geisleri* was not requested from Körber's herbarium at L, but a specimen kept at BM is regarded here as an isotype.

OBSERVATIONS. The only material of *Verrucaria armorica* available at Concarneau was ascomata removed from the substratum. However, the ascomatal structure, asci, and ascospore morphology of this species resemble *Sarcopyrenia gibba* (Nyl.) Nyl. This synonymy was already suggested by Keissler (1938: 264). A second taxon, *Lithosphaeria geisleri*, a facultative synonym of *S. gibba*, was collected in the same locality as *S. beckhausiana* (Germany, Höxter, on sandstone and limestone), and Körber mentioned that both species differed in ascospore morphology despite their external similarity.

During the preparation of this manuscript two Catalan collegues, Navarro-Rosinés & Hladún (1990), studied several collections of material referred to as *Sarcopyrenia gibba* and *Lithosphaeria geisleri* from various herbaria, as well as material collected by themselves from the northeast of Spain. They conclude that two varieties can be recognized within *Sarcopyrenia gibba*: var. *gibba* and var. *geisleri*, and suggested that *S. gibba* var. *geisleri* would be more widely distributed in Europe, whereas var. *gibba* is present in more southern localities.

VII. Excluded or uncertain taxa

The taxa listed below are of uncertain position or are excluded from the genera dealt with here. They are aranged in alphabetical order of the final epithet.

Verrucaria beloniza Stirton in *J. Linn. Soc. Bot.* **14**: 472(1875). *Arthopyrenia beloniza (Stirton) Müll. Arg. in Bull. Herb. Boissier* **2**: 90 (1894). *Leptorhaphis beloniza* (Stirton) Hellbom in *Bih. K. svenska VetensAkad. Handl.* **21** (3/13): 139 (1896). Type: New Zealand, Wellington, 'ad corticem vetustum', *J. Buchanan* (GLAM—holotype; BM!—isotype).

Verrucaria macrocyrtospora Knight in *Trans. Proc. N.Z. Inst.* **16**: 355, tab. 36 (1883). *Arthopyrenia macrocyrtospora* (Knight) Müll. Arg. in *Bull. Herb. Boissier* **2**: 90 (1894). *Leptorhaphis macrocyrtospora* (Knight) Hellbom in *Bih. K. svenska VetensAkad. Handl.* **21** (3/13): 139 (1896). Type: New Zealand, Wellington, 'ad arborum cortices' (WELT!—holotype).

Fig. 57B, 58, 59.

Thallus: Absent.

Ascomata: Perithecioid, globose, black, matt, rugose (moriform), scattered singly, sometimes confluent, 0.5–1 mm diam; spherical, immersed in the bark, becoming completely superficial, with a central ostiole in a small papilla. Wall: continuous and furrowed, dark brown to blackish, incorporating bark material in its lower part, *c.* 40–80 µm thick, becoming completely black towards the edge; composed of thin- walled isodiametric cells, 5.5–10 µm, with dark brown to blackish walls and enlarged lumina forming a pseudoparenchymatous tissue of leptodermatous cells of textura angularis. Hamathecium: of paraphysoids, composed of colourless, smooth, branched and anastomosing, thin-walled hyphae, less than 2 µm wide, with infrequent septa, enveloped in mucus; hymenial gelatin not changing colour in iodine. Asci: arising from the base of the ascomatal cavity, ripening sequentially, cylindricalclavate, 110–170 × 17–22 µm; two wall layers observed, the outer thick and gelatinous, the inner without an apparent internal apical beak; no other apical structures observed; 8-spored; discharge not observed, probably fissitunicate. Ascospores: arranged in one or two bundles in the asci, colourless to yellowish, thick-walled, smooth, sigmoid to curvate, scolecosporous, 85–120 × 3–4.5 µm, attenuated at the apices, 11- or more septate, constricted at the septa, each cell containing numerous refringent particles.

Conidiomata: Not observed.

ECOLOGY. On bark of an unknown host, growing mainly along the furrows, and not causing apparent damage; probably saprobe.

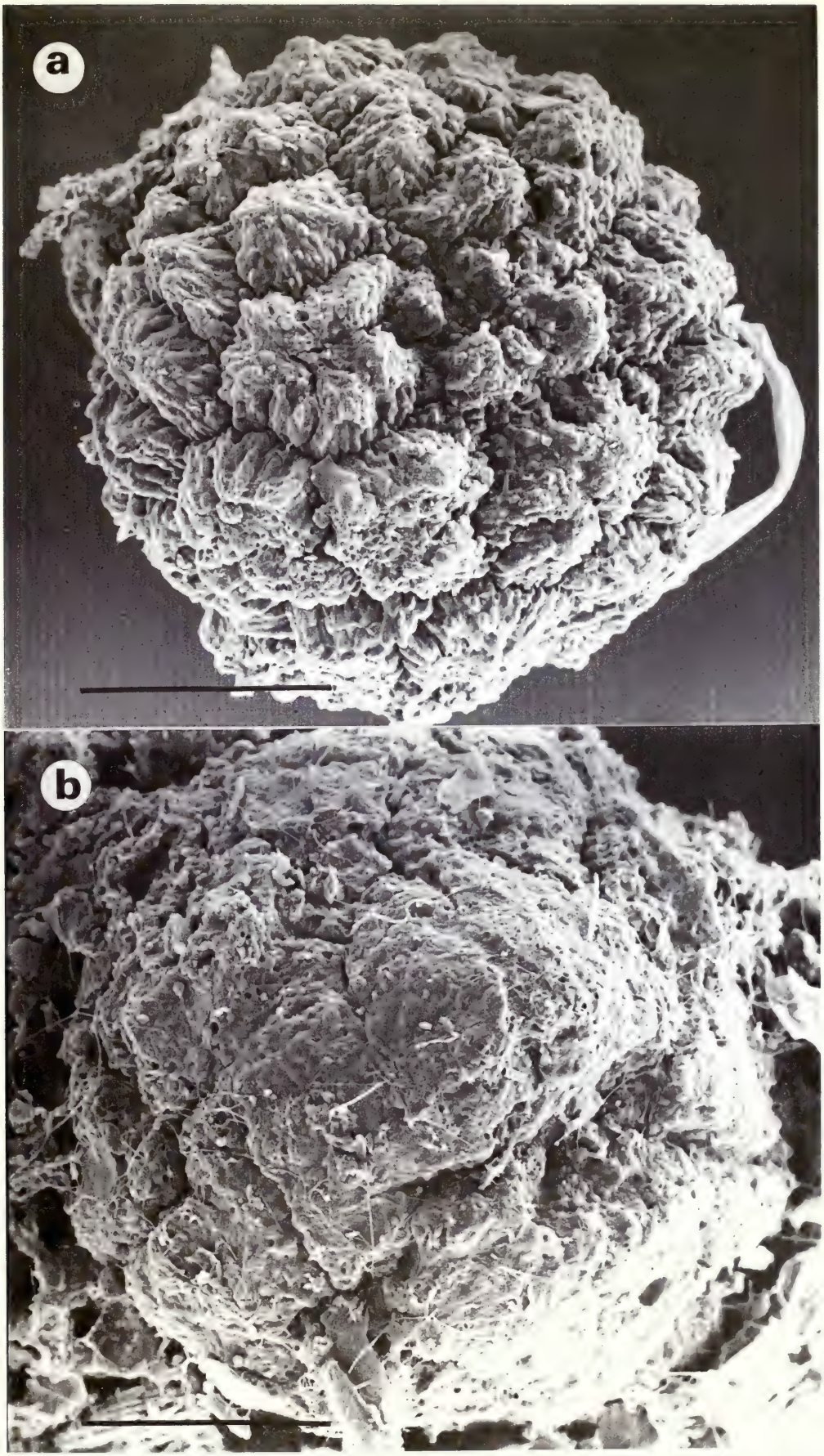


Fig. 57 *Rhytidiella moriformis* Zalasky (IMI 136514) (a) Surface view of ascoma; scale = 136 μm. *Rhytidiella beloniza* (Stirton) Aguirre (BM–isotype): (b) Surface view of ascoma; scale = 120 μm.

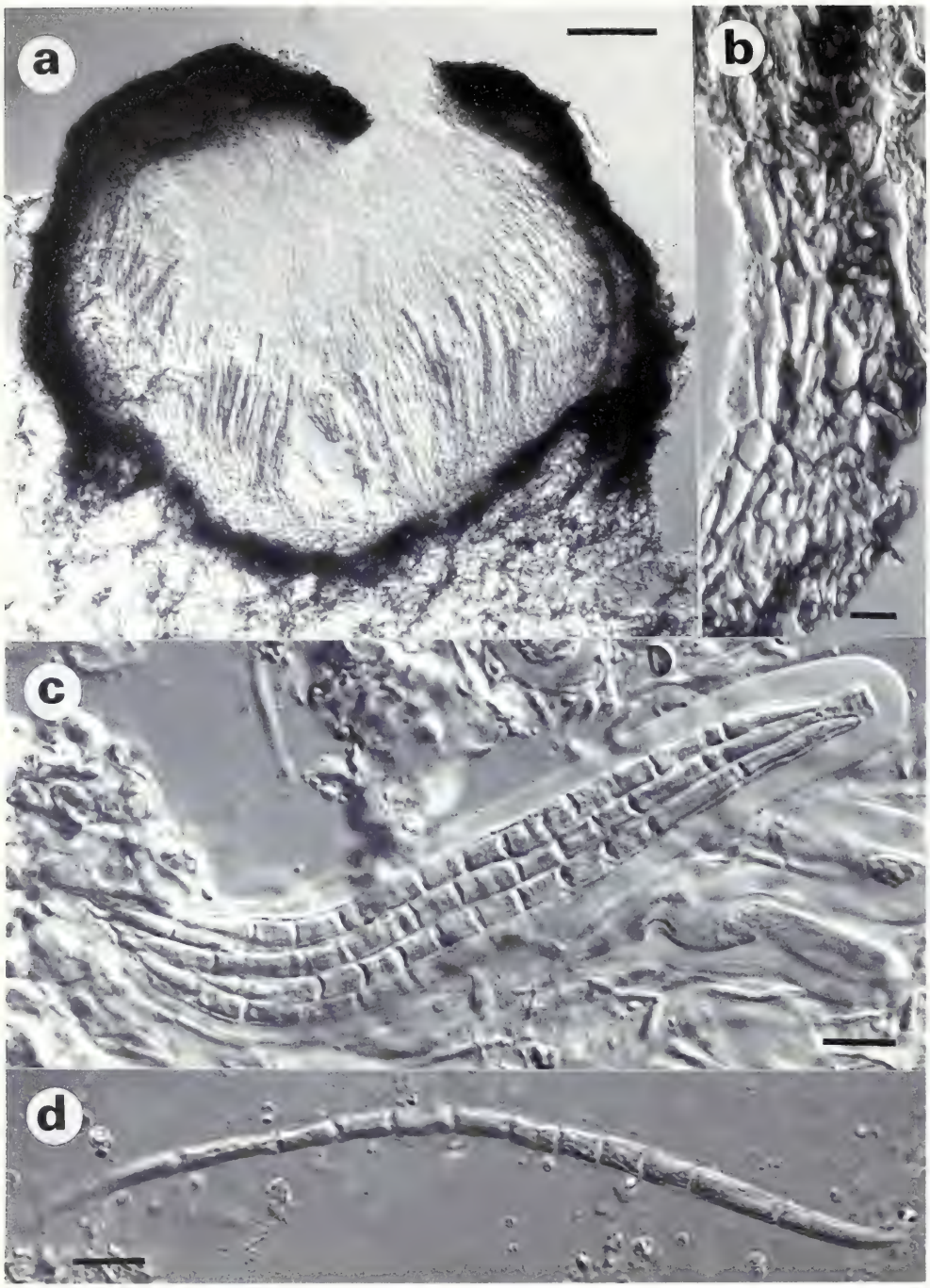


Fig. 58 *Rhytidiella beloniza* (Stirton) Aguirre (BM–isotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of exciple: textura angularis; (c) Ascus and ascospores; (d) Ascospore; scale = 10 μm.

DISTRIBUTION. New Zealand, known only from type locality.

TYPIFICATION. Type material from GLAM was used for the lectotypification of *Verrucaria beloniza* by Galloway (1985: 254). However, since Stirton's herbarium is known to be kept at GLAM (Hawksworth 1974), there was no need to select a lectotype, but the former specimen should be regarded as the holotype (Rollins, 1972: 635; 1980: 509). The holotype collection was not studied, but instead isotype material of the species was obtained from BM. The single collection of *Verrucaria macrocyrtospora* located at WELT is regarded as the holotype.

OBSERVATIONS. Descriptions of both *Verrucaria beloniza* Stirton and *V. macrocyrtospora* Knight were based on different specimens of the same collection as it is shown in the material from WELT, where both specific epithets were handwritten on the same specimen. Both differ from the

genus *Leptorhaphis s. str.* in their ascomatal wall structure as well as ascospore morphology, and therefore should be redisposed elsewhere.

According to ascospore morphology this species seems marginally related to some species of the genus *Ophiobolus* Reiss (Shoemaker, 1976) or *Leptosphaeria* Ces. & de Not. (Walker, 1980), both with scolecosporous ascospores. Certain similarities can be recognized between *Verrucaria beloniza* and the species of the genus *Rhytidiella* Zalasky (1968), and especially with *R. moriformis* Zalasky, type of the genus (for nomenclatural discussion of this species see Eriksson, 1981).

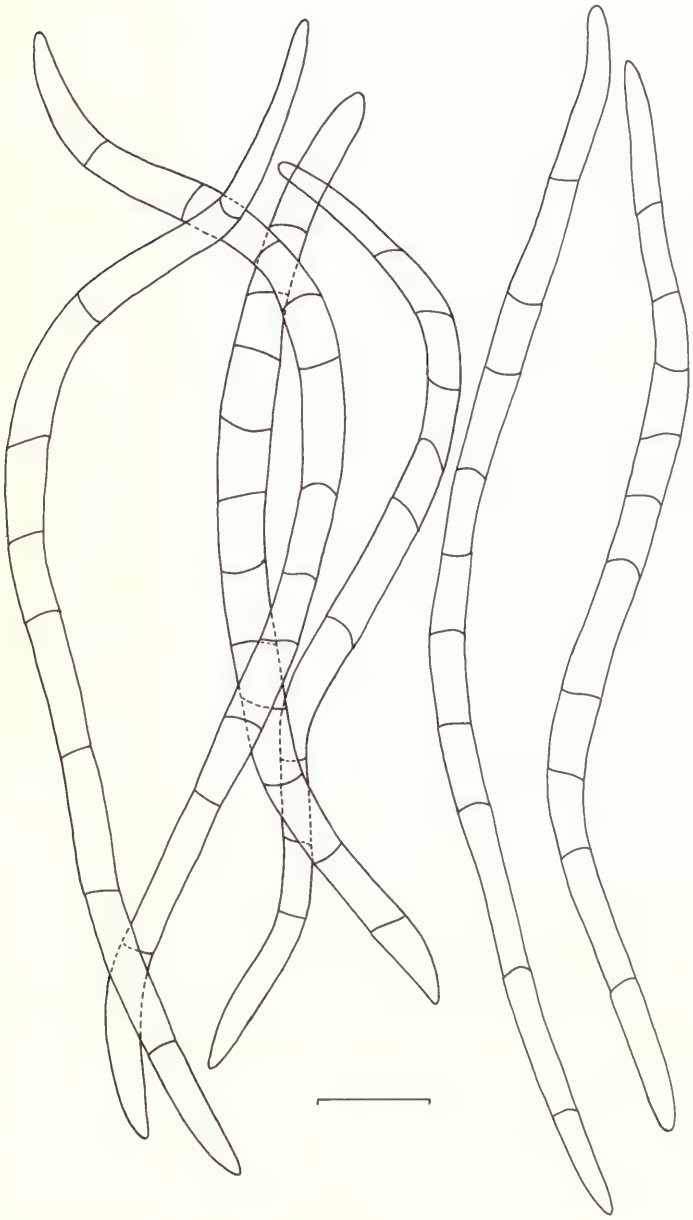


Fig. 59 Ascospore outlines of *Rhytidiella beloniza* (Stirton) Aguirre (BM–isotype); scale = 10 μm.

These similarities are particularly related to ascomatal wall structure, ascus and ascospore morphology and hamathecial tissues. However, it differs from *R. moriformis* in the hymenial gelatin iodine reaction and centrum colouration, as well as pathogenicity. Nevertheless, *Verrucaria beloniza* is here tentatively referred to the genus *Rhytidiella* as **Rhytidiella beloniza** (Stirton) Aguirre, **comb. nov.**, since characteristics such as ascomatal and ascus structure and hamathecial tissues are regarded as taxonomically more significant than centrum iodine reaction.

Whereas both species recognized in the genus *Rhytidiella* until now, *R. moriformis* and *R. baranyany*, are strong pathogens, producing bark cancers on two different species of *Populus* (Zalasky, 1968; Funk & Zalasky, 1974), the third species here accepted behaves as a saprobe, differing from the former in its centrum colour (somewhat colourless) and iodine reaction, and from the latter in having bigger asci and longer ascospores. I have not been able to observe *Phaeoseptoria* anamorphs characteristic of the genus, or other types of conidiomata in the additional species here accepted, but at present it seems appropriate to redispose it in *Rhytidiella*, order Dothideales, for it has been difficult to assign the species satisfactorily elsewhere.

Leptorhaphis candida Steiner *in* Keissler, *Rabenh. Krypt., Fl.* **9** (1/2): 259 (1938). Type: Yugoslavia, Slovenia, 'Zellach bei Veldes', on twigs of *Fraxinus ornus*, 1908, *J. Steiner* (W 5533!—holotype).

Fig. 60, 61.

Thallus: Superficial to immersed fungal mycelium composed of colourless to dark brown, thin-walled, cylindrical and septate hyphae, intermixed with the bark material, extending beyond the ascomata; apparently not associated with algae.

Ascomata: Perithecioid, becoming urceolate, circular, black, shiny, carbonaceous, not pruinose, scattered singly, *c.* 300–600 μm diam; immersed in the bark to half its height, opening by a slightly lateral pore. Exciple: dark brown, covering the hymenium except at the base of young ascomata, becoming marginal, *c.* 60 μm thick, lacking a crystalline layer; composed of more or less isodiametric, thin-walled cells, with enlarged lumina, 2.5–5 μm diam, incorporating bark material in the lowest and more marginal parts of the wall, forming a textura intricata to angularis; leading to a colourless layer of periphysoids, 15–20 μm thick, with a few crystalline inclusions, 5.5–10 μm diam, mainly at the top. Hamathecium: of paraphyses, composed of colourless, smooth, thin-walled and unbranched hyphae, *c.* 1.5 μm wide, septate but not constricted at the septa, and with the apical cell capitate, arising free from the base of the ascomata; periphysoids composed of thin-walled cells, 1.5–2.5 μm thick, the last cell being capitate, growing downwards in young ascomata but becoming and remaining marginal in developed ascomata; hymenial gelatin not changing colour in iodine. Asci: arising from the subhymenium, ripening sequentially, cylindrical, 115–150 × 10–13 μm, short-stalked, apparently unitunicate, thin-walled, becoming thicker at the apex, with an apical cap, 4.5 μm thick, pierced by a narrow pore, not changing colour in iodine; no other apical structures seen; 8-spored; opened asci not observed. Ascospores: arranged in a fascicle, sometimes twisted helically, colourless, thin-walled, smooth, filiform, 150–180 × 2.5–3.5 μm, 12- or more septate, not constricted at the septa, each cell *c.* 6 μm long, without appendages or gelatinous sheaths.

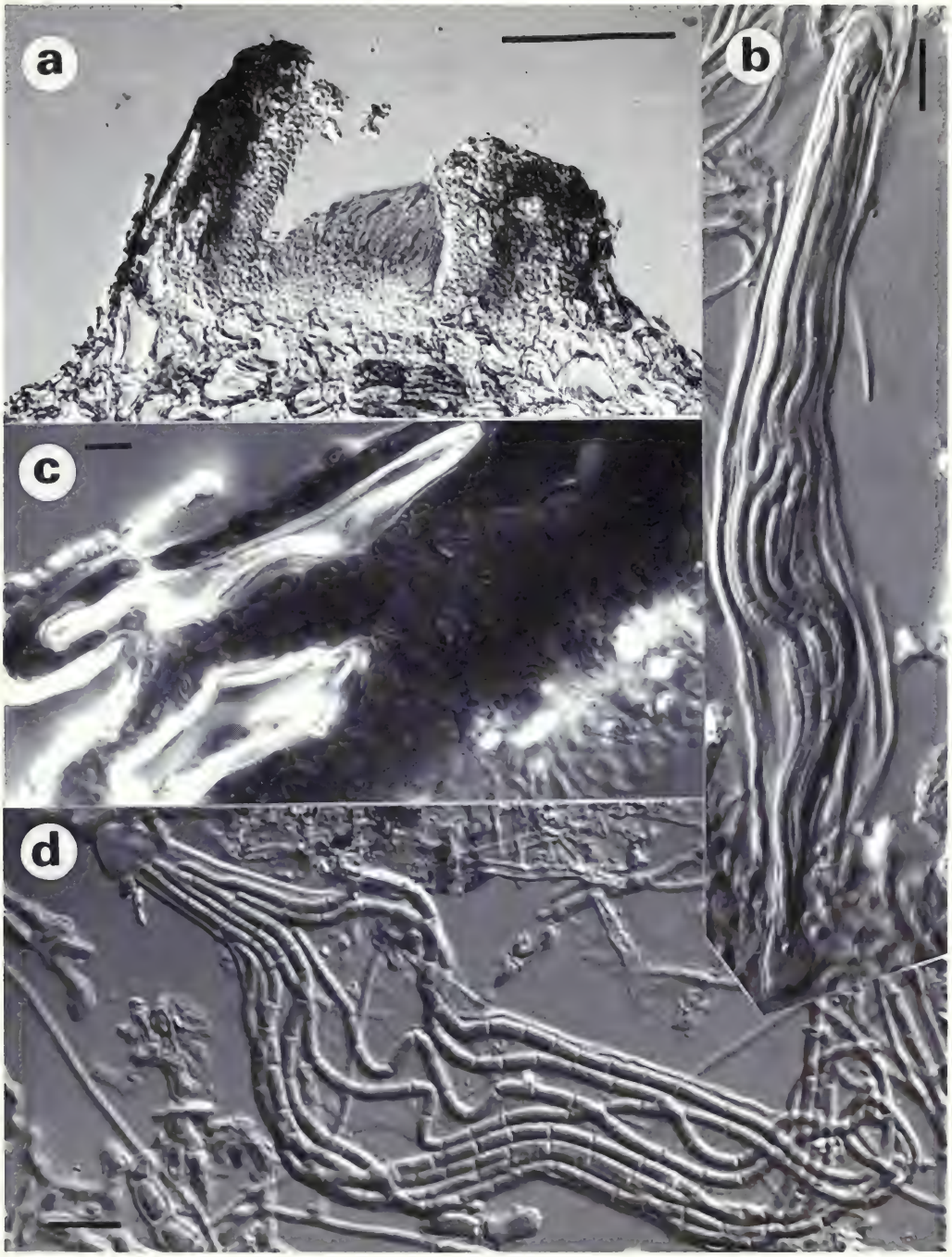


Fig. 60 *Stictis candida* (Steiner) Aguirre (W 5533–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Ascus and ascospores; (c) Detail of exciple: pseudoparenchymatous tissue and host tissue, and crystalline layer; (d) Ascospores; scale = 10 μm.

Conidiomata: Pycnidial, circular, black, shiny, smooth, scattered singly, *c.* 150–250 μm diam; immersed to superficial, opening by an apical pore. Wall: dark brown, *c.* 30–40 μm thick; composed of more or less isodiametric cells, 4–6 μm diam, thin-walled, with dark brown walls and enlarged lumina, mixed with bark material, like the ascomatal wall forming a pseudoparenchymatous tissue of textura globulosa, becoming intricata in places, and containing a crystalline layer towards the pycnidial locule. Conidiogenous cells: colourless, thin-walled, smooth, cylindrical to lageniform, *c.* 6–9 μm in length, apparently enteroblastic, arising from colourless cells about 4.5 μm, adjacent to the conidiomatal wall, which sometimes bear one, two or three conidiogenous cells. Conidia: colourless, aseptate, thin-walled, smooth, obovoid to bacilliform, *c.* 4.5 μm in length.

ECOLOGY. On twigs of *Fraxinus ornus* L., with some *Arthopyrenia* species; not causing any apparent damage; probably

saprophytic. When Keissler (1938: 259) described the species, he observed that trentepohlioid algae were associated with the fungus, but in vertical section I did not observe any fungal-algal association.

DISTRIBUTION. Europe, Yugoslavia, only known from the type locality.

TYPIFICATION. Since only one original collection of this taxon has been located, in W, this is regarded as the holotype.

OBSERVATIONS. On the basis of the ascomatal and ascus structure and morphology, this taxon is a discomycete and must be referred to the family Stictidaceae Fr. (1822), in the order Ostropales. A new combination, **Stictis candida** (Steiner) Aguirre, **comb. nov.**, is introduced here for this fungus, as it differs at the specific level from those treated by Sherwood (1977*a*). It belongs in the section *Cyclostoma*, which includes taxa with filamentous periphysoids, a carbonized exciple, and lack distinct crystalline layers (e.g. *S. fusca* described from North America). However, it differs from the other species included in the section in several features such as ascospore size, iodine reaction, and periphysoids, and from *S. fusca*, in the lack of a prominent margin, grey-pruinose, and lack of iodine reaction.

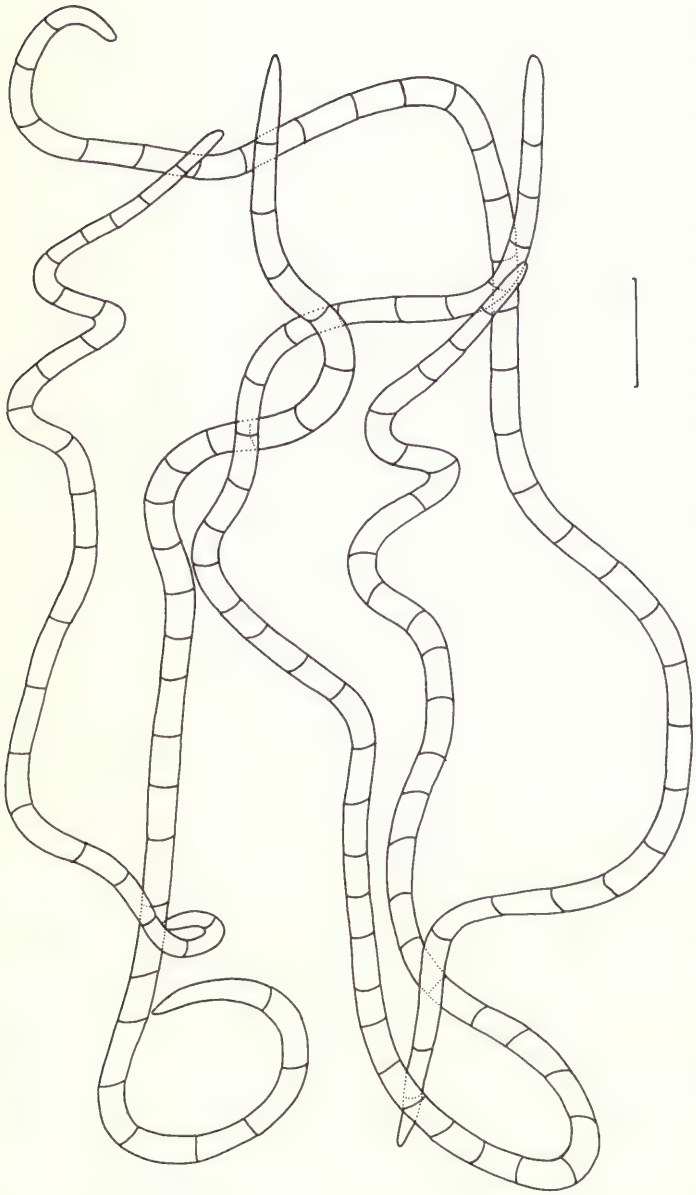


Fig. 61 Ascospore outlines of *Stictis candida* (Steiner) Aguirre (W 5533–holotype); scale = 10 μm.

Ophiobolus inflatus Sacc. & Briard in *Revue mycol.* **7**: 210 (1885). Type: France, Aube, Frayes, on dead branches of *Betula alba*, 27 April 1885, *P. A. Briard* (PAD 2729!—holotype).

Fig. 62, 63.

OBSERVATIONS. Keissler (1938: 243) suggested that, on the basis of ascomata, ascus, and ascospore characteristics, this species might be a taxonomic synonym of *Leptorhaphis quercus* f. *macrospora* Eitner, here treated as *Cresporhaphis macrospora* (p. 149). Comparative studies of the type material of both species showed that both taxa belong to different orders, and that the species described by Saccardo & Briard is really more closely related to the genus *Ophiobolus* sensu Shoemaker (1976) and Walker (1980), or to the genus *Nodulosphaeria* sensu Holm (1957), having ascospores somewhat resembling these of *Nodulosphaeria erythrospora* (Reiss) Holm [syn. *Ophiobolus erythrosporus* (Reiss) Winter], with a swollen cell near the middle and without appendages. Therefore *O. inflatus* should be referred to the order Dothideales, whereas the genus *Cresporhaphis* is considered to be closely related to the order Trichosphaeriales.

Verrucaria kentrospora Branth *in* Grønlund in *Vidensk. Meddel. Naturh. Föreis Kjöbenhavm*: 250 (1874). *Leptorhaphis kentrospora* (Branth) Zahlbr., *Cat. lich. univ.* **1**: 342 (1922). Type: Greenland, Tasermiut, on *Betula*, 1884, *Eberlin* (C!—neotype, selected here).

Fig. 64.

Thallus: Only observed in vertical section, and composed of colourless, thin-walled, smooth hyphae, *c.* 2.5 μm wide, septate and dichotomously branched, not constricted at the septa, loosely associated with chlorococcoid algae.

Ascomata: Perithecioid, small, carbonaceous, ellipsoidal to circular, shiny, smooth, scattered singly, 350–650 μm diam, immersed in the bark, becoming superficial, applanate, dimidiate, with a centrally located ostiole. Involucrellum: greenish-brown or greenish-black, surrounding the centrum except at the base, 30–35 μm thick, turning deep green, later reddish-brown in nitric acid; composed of dark green, thin-walled, smooth hyphae, septate and constricted at the septa, 4.5–5 μm broad, mixed with bark material, forming a clypeus of textura intricata. Hamathecium: of pseudoparaphyses, composed of colourless, smooth, thin-walled and anastomosing hyphae, forming a net, surrounded by mucus; hymenial gelatin amber in iodine. Asci: numerous, arising from the base and angles of the ascomata cavity, ripening sequentially, cylindrical, becoming broader at the base, short-stalked, 50–80 × 11–17 μm; two wall layers observed, the outer wall

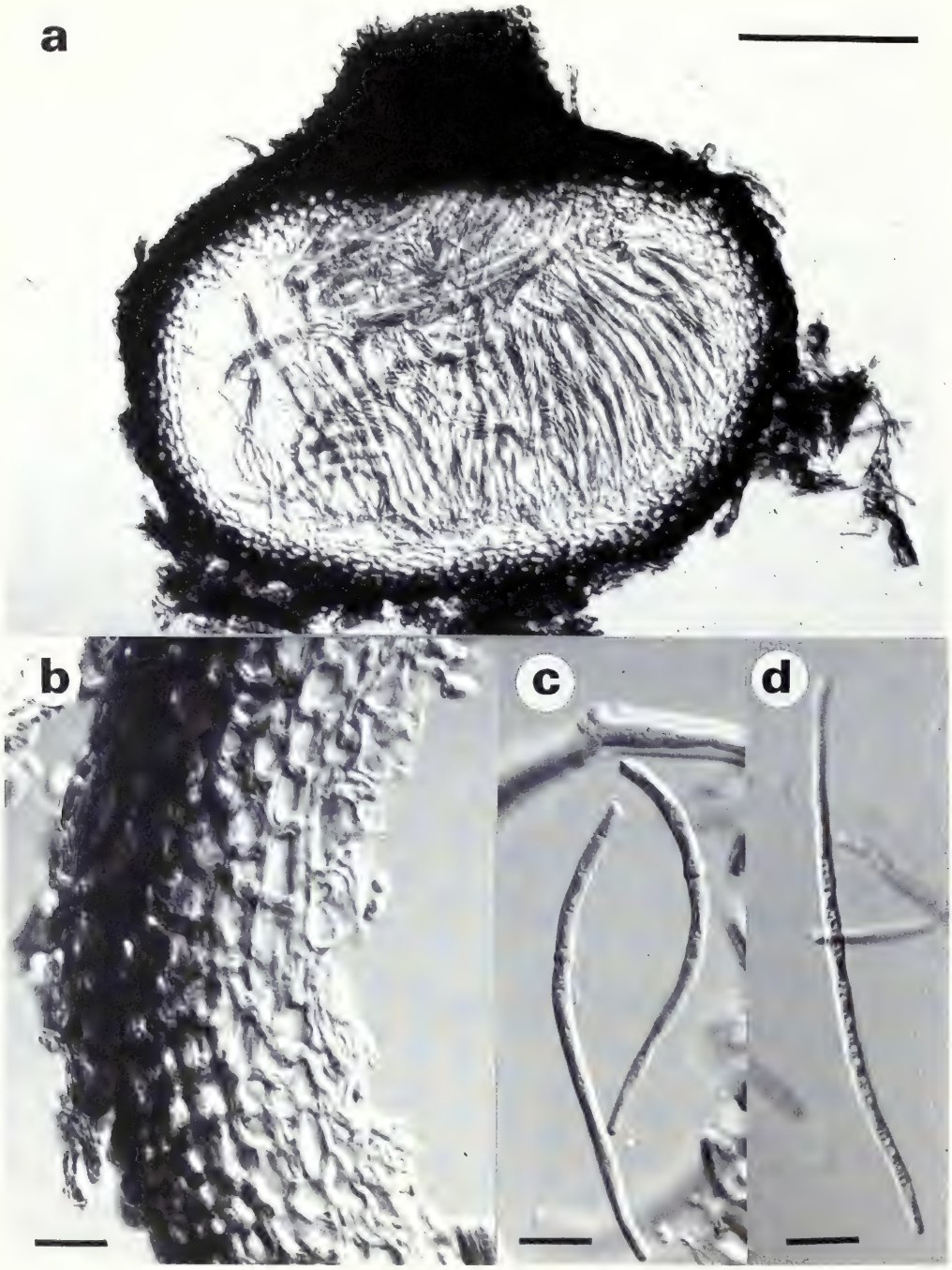


Fig. 62 *Ophiobolus inflatus* Sacc. & Briad (PAD 2729–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of exciple: textura angularis; (c) Ascospores showing swollen sub-median cell; scale = 10 μm.

thin and smooth, the inner without an internal apical beak, truncated at the apex, not changing colour in iodine; no other apical structures seen; 8-spored; discharge not observed. Ascospores: biseriately arranged in the ascus, colourless, thick-walled, smooth, fusiform, 20–25 × 4.5–6.5 μm, 1-, 3- (5-) septate, constricted at the septa, often with one of the middle cells enlarged, with acute apices, without appendages or gelatinous sheaths.

Conidiomata: Not observed.

ECOLOGY. The material of *Verrucaria kentrospora* was growing on *Betula* bark with some lichenized fungi, not causing any apparent damage; it is loosely associated with chlorococcoid algae, but perhaps not lichenized.

TYPIFICATION. Type material of *Verrucaria kentrospora* could not be located at C. However Dr E. S. Hansen found another specimen from Greenland identified by D. Branth as *Verrucaria kentrospora*, which agrees very well with the

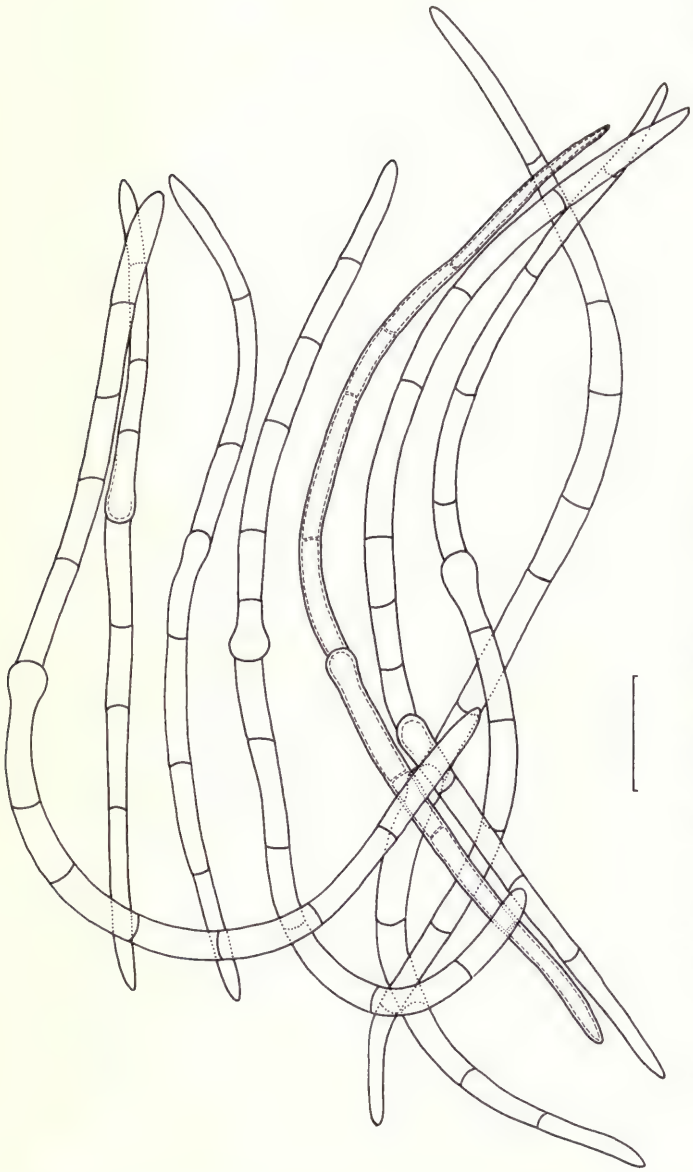


Fig. 63 Ascospore outlines of *Ophiobolus inflatus* Sacc. & Briad (PAD 2729–holotype); scale = 10 μm.

original description of the taxon provided by the author; this is therefore here selected as the neotype for this name.

OBSERVATIONS. After studying authentic material of *Verrucaria kentrospora*, I concluded that the taxon should be referred to the Dothidealean genus *Mycoglaena* Höhnel, on the basis of the ascus and ascospore morphology and the typical colour reaction of the ascomatal wall with nitric acid, changing from greenish-black to deep green, and finally reddish-brown. Harris (1973) in his account of the North American *Mycoglaena* species, included three species which differ mainly in ascospore morphology and septation, and described a new species on *Quercus* bark, which differs from *M. myricae*, in having 5-septate and longer ascospores. I believe that *Verrucaria kentrospora*'s general features resemble those of *M. myricae* (Nyl.) Harris, despite the slightly bigger ascospore size and the occasional presence of 5-septate ascospores; therefore both taxa are here tentatively placed together. Nevertheless type or original material of *M. myricae* was not studied during the course of this research.

Leptorhaphis koerberi ['Körberi'] B. Stein *in* Cohn, *Krypt., Fl. Schles.* **2**(2): 350 (1879). *Ophiobolus koerberi* (B. Stein) Berlese & Voglino *in* Saccardo, *Syll. Fung., Additamenta ad Vol.* I–IV: 190 (1886). *Leptosphaeria koerberi* (B. Stein) Winter, *Rabenh. Krypt., Fl.* **1**(2): 443 (1887). *Metasphaeria koerberi* (B. Stein) Schröter *in* Cohn, *Krypt., Fl. Schles.* **3**(2): 355 (1894). *Leptosphaeria quercus* f. *koerberi* (B. Stein) Eitner in *Jber. schles. Ges. vaterl. Kult.* **78**(2): 25 (1901) ['1900']. *Sagediopsis koerberi* (B. Stein) Clem. & Shear, *Gen. Fungi*, 272 (1932). Type: Poland, Silesia, Riesengebirge, Hirschberg, 'auf der meist gar nicht veränderten kruste von *Koerberiella wimmeriana* am Basalt der kleinen Schneegrube (St.)'.

OBSERVATIONS. No authentic material of this taxon was located in WRSL, W, B or WU. However, Keissler (1930: 515–516) placed this lichenicolous taxon as a synonym of *Ophiobolus barbarus* (Th. Fr.) Keissler, together with *Leptorhaphis steinii*. He also observed that *L. körberi* and *L. steinii* were collected at the same locality on a similar substratum, and they only differed in that *L. koerberi*'s spores were needle-shaped with a thickened last cell, whereas *L. steinii*'s spores were fusiform. I have not seen original material of *L. koerberi*, but the biological characteristics of the taxon, i.e. a lichenicolous fungus, suggest that *L. koerberi* is not closely related to *Leptorhaphis*, which includes only saprophytic or perhaps loosely lichenized taxa.

Also unable to locate the type of the species Triebel (1989: 112) selected a neotype from material collected by Stein in the Sudetes, Poland, as early as 1872. She also found that this was closely related to *Gongylia aquatica* Stein, and transferred both taxa to the lichenicolous genus *Sagediopsis* as *S. aquatica (Stein) Triebel.*

Lahmia kunzei Körber, *Parerg. lich.*: 282 (1861). *Calicium kunzei* Flotow, '*in litt. ad* Rabenhorst (1850)'; nom. inval. (Art.32.1). *Pragmopora kunzei* (Körber) Cohn, *Krypt., Fl. Schles.* **2**: 128(1893). Type: Poland, Silesia, Hirschbergam, Sattler Valley, 'in fissuris corticis *Populi tremulae*', *G. W. Körber* [Körber, *Lich. Sel. Germ. exs.* no. 140, as *Lahmia kunzei* (Fw.) Körber] (B 59624!—syntype).

Parkerella populi A. Funk in *Can. J. Bot.* **54**: 868 (1976). Type: Canada, British Columbia, Williams Lake, 'in *Populo tremuloide*', 15June 1973 (DAVFP 20871)

Fig. 65.

TYPIFICATION. Körber (1861: 232) published that the basionym of *Lahmia kunzei* was a *Calicium* species mentioned in a personal letter received from Rabenhorst in 1850, later named by this author as *Calicium mosigii*. To my knowledge, in that year Rabenhorst only published several articles referring to lichens in *Flora, Jena* **33**: 359, 374, 531, where one or two species of *Calicium* were mentioned, but none of them related to *Calicium kunzei* or *C. mosigii*; consequently the

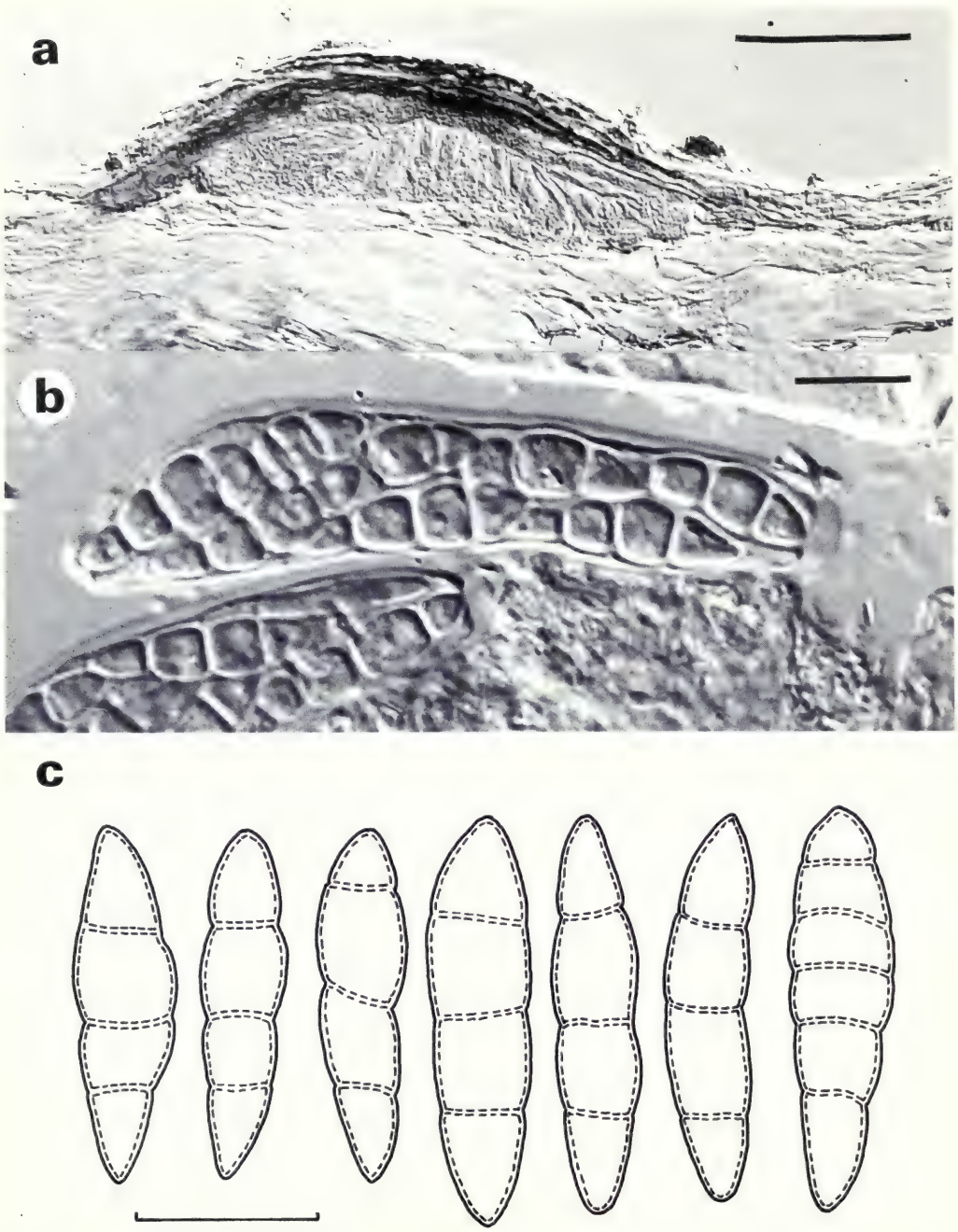


Fig. 64 *Mycoglaena myricae* (Nyl.) Harris (C–neotype of *Verrucaria kentrospora*) (a) Vertical section of ascoma; scale = 100 μm; (b) Ascus and ascospores, inner wall showing ocular chamber; (c) Ascospore outlines; scale = 10 μm.

species is regarded here as not validly published according to Art. 32.1.

OBSERVATIONS. Zahlbruckner (1932: 93) placed this species as a taxonomic synonym of *Leptorhaphis lucida* Körber, following Vainio's (1921: 188) criteria. The latter, in his observations on *Campylacia*, believed that both *L. lucida* and *Lahmia kunzei* were closely related and belonged to the discomycetes. However, Keissler (1938: 257) disagreed with these criteria and pointed out that *Lahmia kunzei* was a non-lichenized discomycete, which according to Nannfeldt (1932: 324) should be included in the order Lecanorales, whereas *Leptorhaphis lucida* was a pyrenocarpous lichen. Recently, Eriksson (1986: 347–360) has carefully studied the species, and provided a detail description. He considered the species not to be closely related to any other fungus, and thus proposed the new family Lahmiaceae, and the new order Lahmiales. Material of this species has also been misidentified as *Leptorhaphis atomaria* (Ach.) Szat., also occurring on *Populus* bark, in several collections studied.

ADDITIONAL SPECIMENS. **Austria**, Samland, Galtgarben, on

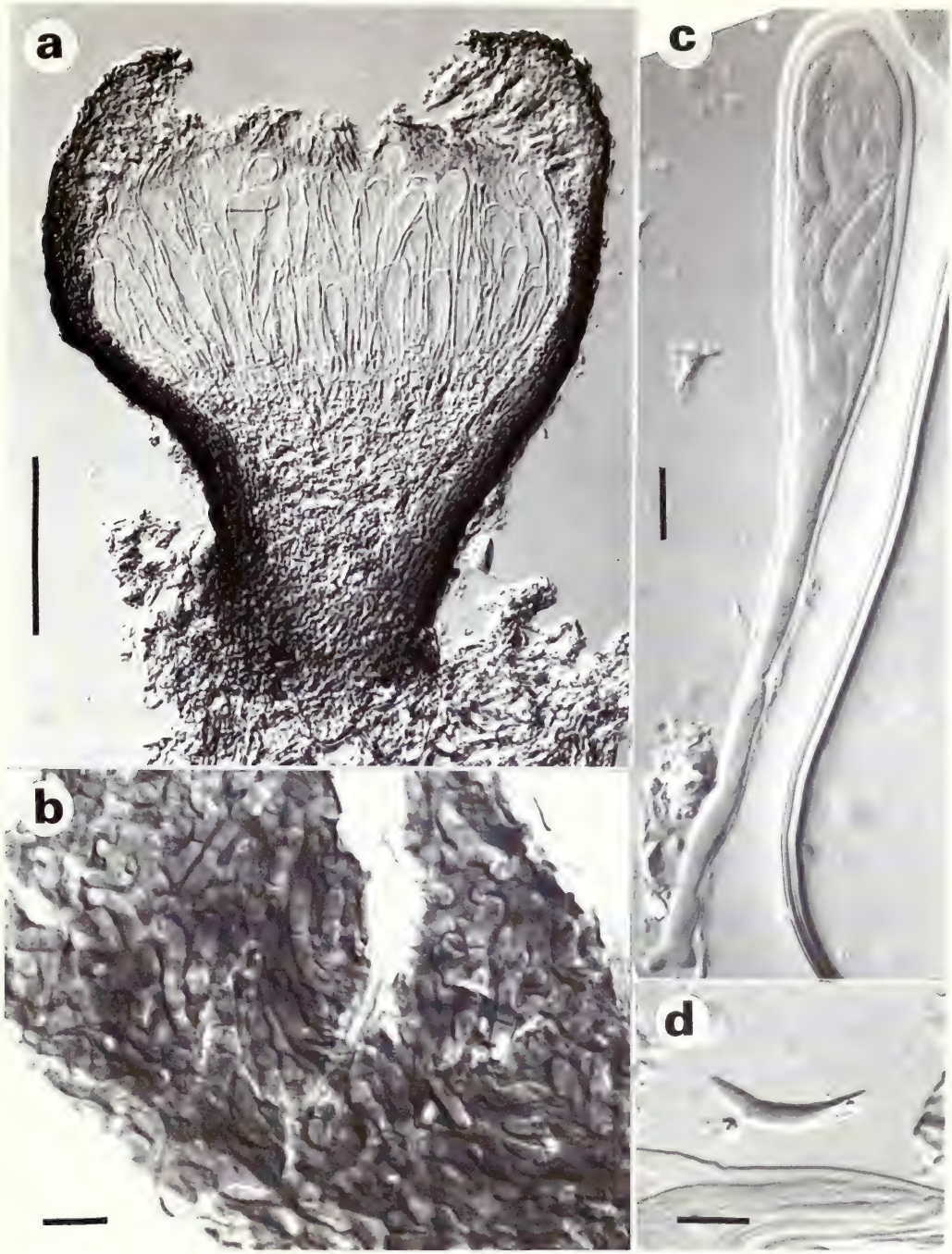


Fig. 65 *Lahmia kunzei* Körber (IMI 322591) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of wall: textura intricata; (c) Ascus and ascospores; (d) Ascospore; scale = 10 μm.

Populus tremula, 23 August 1902, *G. Lettau* (B 59706). **Germany**, Wesfalia, Höxter,Solling, on *Populus tremula*, May 1860, *C. F. L. Beckhaus* (B 59716). Marienmünster, on *Populus tremula*, *C. F. L. Beckhaus* (B 59726). Münster, 'Glorkmuburg', on *Populus*, September 1861, *T. R. J. Nitschke* (B 59727). Dörnthe, Ibbenbüren, . . .[illegible], on *Populus alba*, June 1861 (B 59623). **Norway**, Finnmark, Karasjok, 'ad Arrebakle', 1866, *J. M. Norman* (O). Akershus, Asker paroch., 'Grenfserråsen', 30 April 1871, *J. M. Norman* (O). Akershus, Oslo, Skóien, 9 April 1871, *N. G. Moe* (O). Akershus, Asker paroch., between Raunsborg and Asker, *J. M. Norman* (O). . . . 'Sæm, Snaasm paroch.', *J. M. Norman* (O). Vestfold, Larvik, Tiredriksvamreier, 27 January 1882, *J. M. Norman* (O). **Poland**, Handorf, on *Populus tremula*, June 1868, *P. Wienkamp* (B 44682). **Sweden**, Västerbotten, Vännäs paroch., *c.* 1 km E of Harrselsfors Power Station, E slope of the Ume River, on *Populus tremula* (bark with deep fissures), 18 May 1986, *O. Eriksson* (IMI 322591). ex herb. Swartzii (UPS). [Sine loc.], on *Populus alba*, *T. R. J. Nitschke* (B 59694).

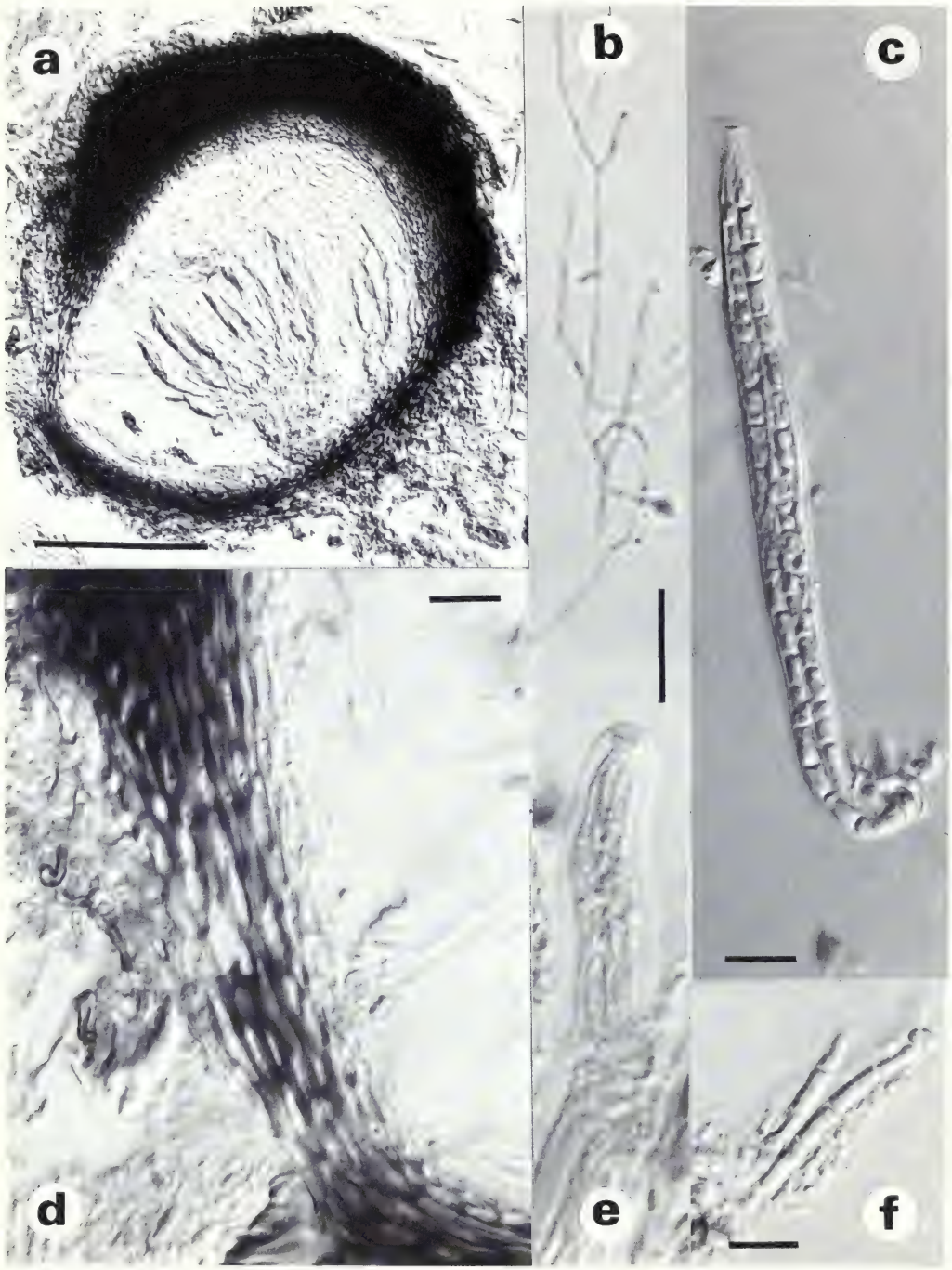


Fig. 66 *Porina borreri* (Trevisan) D. Hawksw. & James (Concarneau–holotype of *Verrucaria longispora*) (a) Vertical section of ascoma; scale = 100 µm; (b) Branching paraphyses; (c) Ascus and ascospores; (d) Detail of exciple: textura porrecta; (e) Detail of ascus apex; (f) Ascospores; scale = 10 µm.

Leptorhaphis leptogiophila Minks *in* G. Winter in *Flora, Jena* **60**: 211 (1877). *Leptosphaeria leptogiophila* (Minks) Winter, *Rabenh. Krypt., Fl.* **1**(2): 443 (1885). *Metasphaeria leptogiophila* (Minks) Berlèse & Voglino *in* Sacc., *Syll. Fung., Additamenta ad vol.* I–IV: 158 (1886). *Physalospora leptogiophila* (Minks) Vouaux in *Bull. Soc. mycol. Fr.* **29**: 82 (1913). Type: Switzerland, Gossau, Hegetschweiler, 'von *Physma franconium*'.

OBSERVATIONS. Type material was not available at B and JE herbaria. No ascospore details were given in the protologue; however, according to Vouaux (1913: 82) and Keissler (1930: 485) these are narrowly fusiform, 16–17 × 3–4 µm, 3-septate, and attenuated at the apices. Moreover, according to a more recent description of the species provided by Santesson (1960: 509) from material collected in northern Spain, the ascomatal structure, hymenium, ascus morphology as well as the

ecological preferences differ from those in *Leptorhaphis*; therefore this taxon should be referred elsewhere. As in many other lichenicolous fungi with transversely septate, colourless ascospores, it has been suggested that it should be more appropriately referred to *Metasphaeria* (Keissler, 1930, 1938) or to *Physalospora* (Vouaux, 1913). Santesson (1960) preferred the latter and included the taxon in *Physalospora* after studying several specimens, always on *Collema subfurvum*, from Norway and Spain and kept at UPS.

Verrucaria longispora P. Crouan & H. Crouan, *Fl. Finist.*: 86 (1867). *Leptorhaphis longispora* (P. Crouan & H. Crouan) Boistel, *Nouv. Fl. Lich.* **2**: 287 (1903). Type: France, Brittany, Finistère, 'sur ecorce de chêne', *P. L. & H. M. Crouan* (Concarneau!—holotype)

Fig. 66. 67A.

Thallus: Smooth, olivaceous-grey, crustaceous, thin, matt, continuous, not surrounded by a prothallus; superficial to immersed in the bark, composed of colourless to brown, thin-walled, smooth, cylindrical hyphae, associated with more or less isodiametric, chlorococcoid algae, *c.* 10 µm diam.

Ascomata: Perithecioid, globose, carbonaceous, smooth, scattered singly, numerous, *c.* 250 µm wide and 300 µm high; immersed in the substratum, only apically superficial, with a centrally located ostiole. Wall: continuous, dark brown, *c.* 40 µm thick, becoming thicker and darker in the upper part towards the surface and near the ostiole; composed of isodiametric cells, *c.* 3–3.5 µm diam, with enlarged lumina, brown and thick-walled, becoming colourless towards the centrum, forming a textura globulosa. Hamathecium: of paraphyses, composed of colourless, smooth, branching, thin-walled hyphae, *c.* 1.5 µm broad, septate, not constricted at the septa, free at the apices, enveloped in mucus; hymenial gelatin not changing colour in iodine. Asci: arising from the base of the ascomatal cavity, ripening sequentially, cylindrical, short-stalked, 65–95 × 7–9.5 µm, two very thin wall layers observed, the outer wall smooth, the inner only thickening at the apex, which is truncated and stains deeper in cotton-blue, but not changing colour in iodine; 8-spored; discharge not observed. Ascospores: biseriately arranged in the ascus, colourless, thin-walled, smooth, fusiform, sometimes sigmoid, 30–45 × 3–4 µm, 3-, 7-septate, not constricted at the septa, attenuated at the apices, without appendages or gelatinous sheaths.

Conidiomata: Not observed.

ECOLOGY. On rough bark of *Quercus robur* L., growing with *Enterographa crassa* (DC) Fée, presumably in old woodlands of temperate regions, not causing any apparent damage; lichenized with an unidentified chlorococcoid photobiont.

OBSERVATIONS. Ascus morphology and centrum structure in this taxon resemble those of the Trichotheliaceae (Müll. Arg.) Bitt. & Schill., in the Pyrenulales (Eriksson 1981: 160), and the material studied recalls a taxon described by Swinscow (1962: 26) as *Porina olivacea* (Pers.) A. L. Sm. [i.e. *Porina borreri* (Trevisan) D. Hawksw. & James]. Type material of the latter studied at BM comfirms this resemblance, but unfortunately our species seems to be associated with green algae other than *Trentepohlia*. In the same work, Swinscow included some other species in *Porina*, such as *P. affinis* (Massal.) Zahlbr. [i.e. *Strigula affinis* (Massal.) Harris] and *P. faginea* (Schaerer) Arnold [i.e. *S. stigmatella* (Ach.) Harris], which were later regarded by Harris (1975) as species of the genus *Strigula*, having an apical dimple in the inner wall of the asci. Since the asci in *Verrucaria longispora* cannot be regarded as'bitunicate', and no apical dimple was observed in the inner wall, the taxon is here provisionally referred to the genus *Porina*, as *P. borreri* (Trevisan) D. Hawksw. & James, although this needs further study to elucidate whether the taxon presents or not *Trentepohlia* algae.

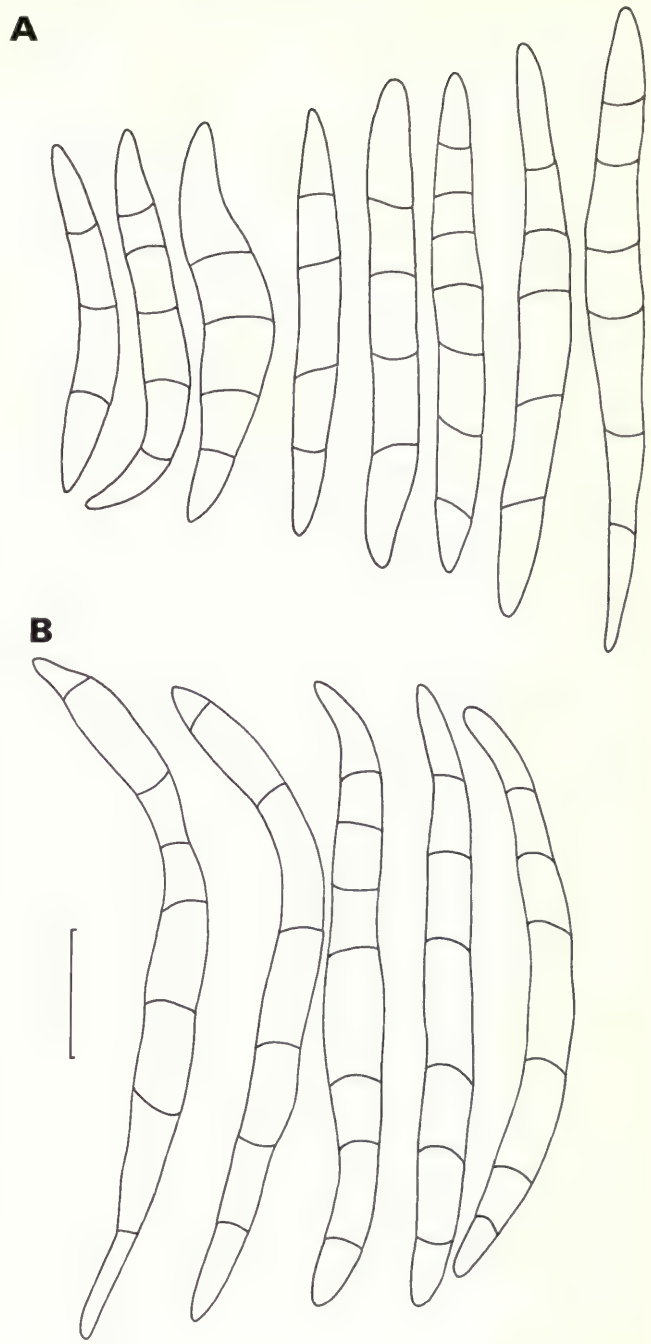


Fig. 67 Ascospore outlines (A) *Porina borreri* (Trevisan) D. Hawksw. & James (Concarneau–holotype of *Verrucaria longispora*); (B) *Capronia longonigra* (Norman) Aguirre (UPS–holotype); scale = 10 µm.

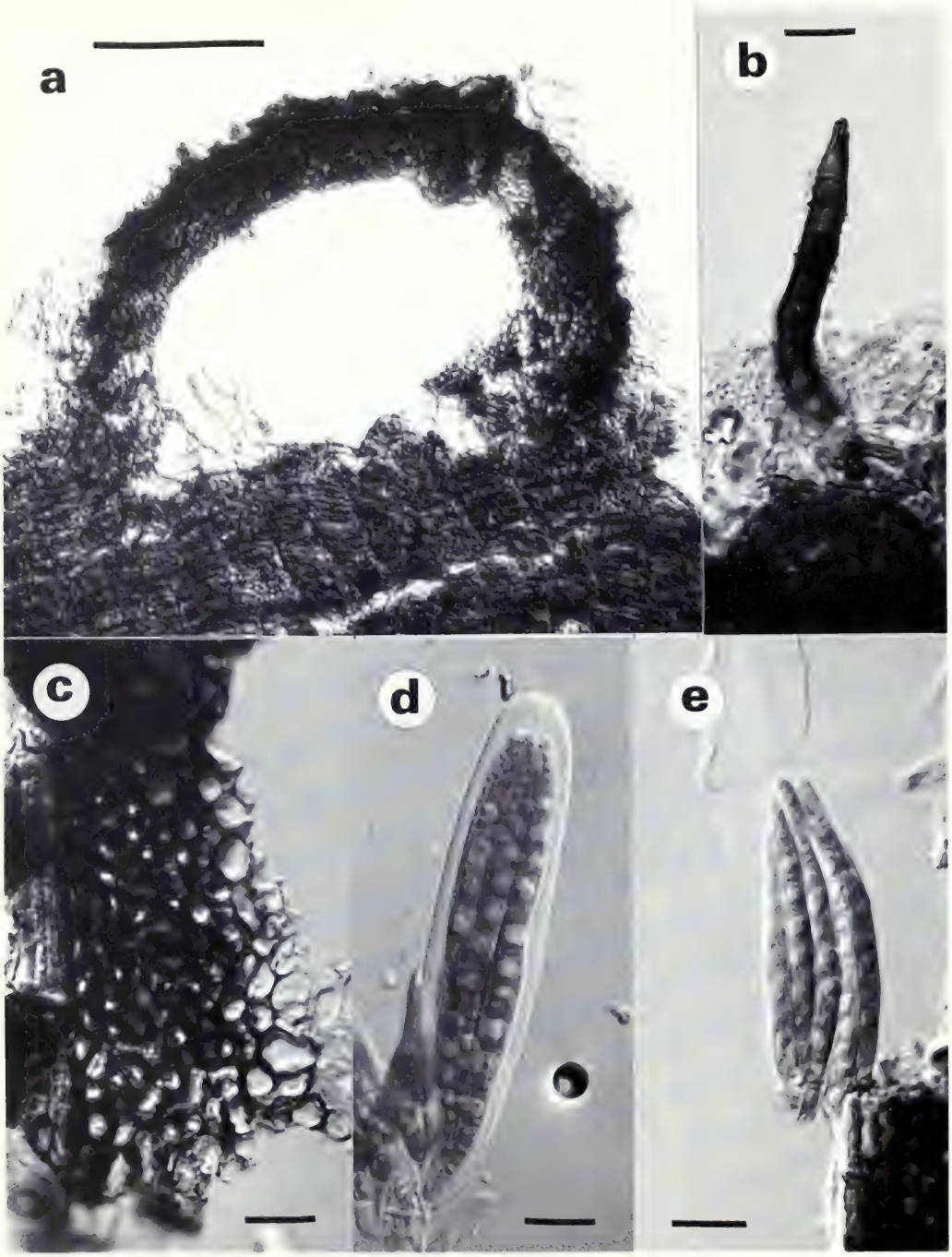


Fig. 68 *Capronia longonigra* (Norman) Aguirre (UPS–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Detail of chetae; (c) Detail of exciple: textura angularis; (d) Ascus and ascospores; (e) Ascospores; scale = 10 μm.

Leptorhaphis longonigra Norman in *Ofvers. K. VetenskAkad Förh. Stockh.* **41**(8): 41 (1884). Type: Norway, Bodö, Kvalvaag, on trunks of *Alnus glutinosa*, 20 June 1879, *J. M. Norman* (UPS!—holotype).

Fig. 67B, 68.

Thallus: Inconspicuous to blackish, continuous, not well delimited; superficial, thin, *c.* 45 μm in height; consisting of colourless to brown, thick-walled hyphae, *c.* 2–4 μm wide, constricted at the septa; associated with trentepohlioid algae, *c.* 7–10 μm wide.

Ascomata: Perithecioid, dark brown to black, matt, surface irregular, 300–400 μm diam, scattered singly; superficial, almost spherical, slightly flattened at the base, dimidiate, *c.* 200 μm high; ostiole centrally located. Wall: reddish-brown to black, *c.* 55–60 μm thick, irregular and setose, with thick-walled setae *c.* 40 × 7 μm, apparently non-septate; consisting of isodiametric cells, *c.* 5–7 μm diam, with reddish-brown,

thin and smooth walls and large lumina, forming a textura angularis, only intermixed with bark cells at the sides of the ascomata near the surface. Hamathecium: of paraphyses, composed of colourless, thin-walled, smooth hyphae, *c.* 2 µm wide, cellular, not constricted at the septa, numerous, not branching nor anastomosing; periphyses or periphysoids not observed; hymenial gelatin turning bluish in iodine. Asci: arising from the base and angles of the ascomatal cavity, numerous, ripening sequentially, cylindrical-clavate, short-stalked, 70–80 × 10–15.5 µm; two wall layers observed, the outer thin and smooth, the inner becoming gradually thicker towards the apex, which is pointed, not changing colour in iodine, no other apical structures seen; 6–8 spored, discharged asci not observed. Ascospores: arranged in one or two bundles in the asci, colourless to yellowish, fusiform, with rounded apices, 50–60 × 3.5–4.75 µm, brownish and smooth-walled, 5-, 7-septate, not constricted at the septa, each cell containing 2–3 refringent oil drops; appendages or gelatinous sheaths not observed.

Conidiomata: Not observed.

ECOLOGY. On bark of *Alnus glutinosa*'s trunks; presumably a saprobe, although trentepohlioid algal cells were also observed on the surface associated with fungal hyphae.

DISTRIBUTION. Europe, Norway; known only from type collection.

TYPIFICATION. The taxon does not present any typification problems since only one collection from the original locality was located at UPS, which is regarded as the holotype.

OBSERVATIONS. Characteristics such as the structure of the wall, with a textura angularis, the presence of setae, the structure of the hamathecium (with true paraphyses not pseudoparaphyses), the ascus apical structure (pointed rather than truncate), and the morphology and colour of the ascospores (multiseptate, fusiform, with brownish walls, not colourless and 1- to 3-septate), indicate that this taxon cannot be included within the genus *Leptorhaphis*. Such characteristics are somewhat reminiscent of the family Herpotrichiellaceae Munk (von Arx & Müller, 1975: 126; Eriksson, 1981: 72), which includes genera with superficial, globose to subglose, setose ascomata, sessile asci, with a thin ectotunica and thicker endotunica towards the apex. Recently, Müller et al. (1987: 72) have limited the family to two genera: *Acanthostigmella* v. Höhn and *Capronia* Sacc., which according to Barr (1977: 17) could be segregated on the colour of the ascomata, ascospores and mycelium, being lighter in *Acanthostigmella*.

'Leptorhaphis' longonigra may well be closely related to the genus *Capronia*, although it does not seem to agree with any of the species studied by Müller et al. (1987), and differs also in the structure of the hamathecium with numerous paraphyses and the absence of periphyses or periphysoids in the ostiolar region, while in *Capronia* short periphyses are present in the ostiolar canal, and the hamathecium lacks sterile filaments. Nevertheless the taxon is here tentatively referred to the Herpotrichiellaceae, as **Capronia longonigra** (Norman) Aguirre, **comb. nov.**, although further studies are required when more material is available and the nature of the anamorph is identified.

Leptorhaphis michaudi B. de Lesdain, *Feuille jeun. Nat.* IV, **37**: 71 (1907). Type: France, Provence, Var, Giens, 'sur un Olivier'.

OBSERVATIONS. No authentic material of this taxon is available since Bouly de Lesdain's personal herbarium was destroyed in 1940 (see Hawksworth, 1974; Laundon, 1979). Material was also requested from GL, O and UPS herbaria, which have a few duplicates he sent to colleagues, but without success. Two other *Leptorhaphis* species have been described on olive trees in the mediterranean region: *L. oleae* Massal. (1855) from Italy, and *L. epidermidis* var. *olivetorum* G. Samp. (1923) from Portugal. I have not seen type material of the latter, but the description suggests that both species are rather similar, and do not resemble *L. michaudi*, which according to Bouly de Lesdain (1907) '... diffère du *L. oxyspora* Krb. par ses apothecies arrondies, ses thèques ventrues et par ses spores souvent semi circulaires', whereas in the genus *Leptorhaphis* the ascospores are always fusiform-curvate, instead of semicircular, and the ascomata are dimidiate. I therefore disagree with Keissler (1938: 250–251) who placed *L. michaudi* as a synonym of *L. oleae* on the basis of their complete ascomata; however the application of the name remains uncertain.

Verrucaria byssacea var. **minutissima** Ach., *Meth. Lich.*: 118 (1803). *Thrombium sticticum* var. *minutissimum* (Ach.) Hepp, *Flecht. Eur.* **8**(15): 55, no. 478 (1857). *Verrucaria oxyspora* var. *minutissima* (Ach.) Garov., *Tent. Dispos.*

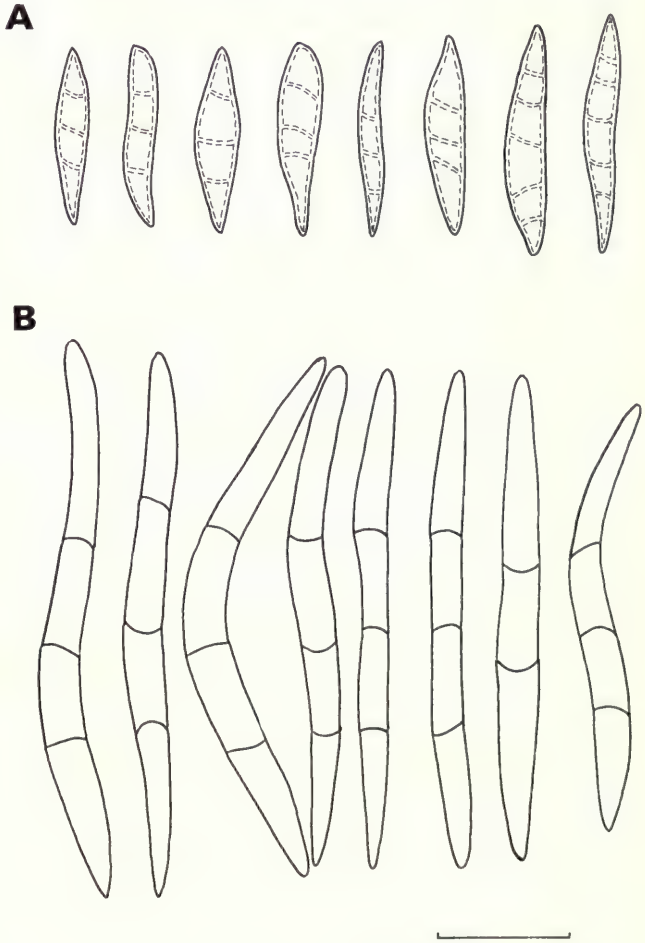


Fig. 69 Ascospore outlines (A) *Verrucaria byssacea* var. *minutissima* Ach. (BM–ACH 312–isotype); (B) *Lahmiomyces piceae* (Anzi) Tom. & Cif. (BM–isotype of *Lahmia piceae*); scale = 10 µm.

Lich. Langob. **10** 1(3): 28 (1865). *Verrucaria albissima* var. *minutissima* (Ach.) Malbr. in *Bull. Soc. Amis Sci. nat. Rouen* **5**: 316 (1869). Type: Sweden, 'in squamis laevigatus cort. *Pini sylvestris* et ligno subputrido *Salicis*', *E. Acharius*, (BM–ACH 312!—isotype).

Fig. 69A.

OBSERVATIONS. Garovaglio (1865) and Malbranche (1869) introduced this taxon as a variety of *Leptorhaphis epidermidis* (Ach.) Th. Fr., and this was later used as a synonym of *L. quercus* by Zahlbruckner (1922: 344) or *L. tremulae* according to Keissler (1938: 254). However the type specimen is not closely related to the genus *Leptorhaphis*, but is a member of the Strigulaceae Fr. The origin of this confusion is presumably Hepp's exsiccate no. 478, on bark *Populus tremula* L., containing ascospores of a species referable to *Leptorhaphis*, which I identified as *L. lucida*, and closely related to *L. tremulae* and *L. atomaria*, also on *Populus* bark. Additional specimens studied from Hue's herbarium in PC, HUE 544 as *Verrucaria minutissima* and HUE 3505/1 as *V. albissima*, are also mixtures of *Leptorhaphis atomaria* and the coelomycete *Pseudoseptoria* sp. As Hepp did not intend to describe a new taxon, but merely misapplied Acharius' name, the epithet must be typified by Acharius' material, and so is tentatively placed in the Strigulaceae. It might be an additional species of the genus *Strigula*.

Leptorhaphis novae-guineae Szat. in *Ann. Hist. nat. Mus. natn. Hung.* **7**: 17 (1956). Type: New Guinea, Berlinhafen, 'in insula Seleo, ad ram. arb.', 4 July 1896, *L. Biró*.

OBSERVATIONS. Type material of the species was requested from BP, where Szatala's herbarium is kept (Hawksworth, 1974; Laundon, 1979), but was not located. Nevertheless it seems unlikely, looking at the location of the species (New Guinea), that it could be referable to the genus *Leptorhaphis*, which on the basis of its species distribution could be regarded as a fungus common in the temperate Northern Hemisphere. Other species with a more tropical distribution, long, filiform, and multiseptate ascospores, previously referred to *Leptorhaphis*, have been here included in a separate genus: *Celothelium* Massal. This taxon could be regarded perhaps as an additional species of this genus. However, the ascospores were described as being 1-septate and in several bundles in the ascus: 'Sporae in ascis polystichae, aciculares, 1-septatae vel simplices, spiraliter contortae, apicibus acutis, 54–64 mikr. longae et 2–3.5 mikr. latae', instead of multiseptate and in one fascicle like in *Celothelium*.

Leptorhaphis epidermidis var. **olivetorum** G. Samp. in *Bolm Soc. broteriana* II, **2**: 4 (1923). Type: Portugal, Coimbra, Penedo da Saüdade, 'cascas das oliveiras', January 1922, *G. Sampaio*; Obidos, June 1918, *A. R. Jorge*.

OBSERVATIONS. Type material of the species was requested from but not located in the Instituto de Botânica 'Dr. Gonçalo Sampaio' in Porto (PO; Prof. R. Salama, in litt.). According to the taxon's description of ascomata, asci and ascospore morphology, size, and number of septa: '... peritécias de pirénio demidiado, com paráfises um pouco espessas e ramosas ... esporos livres arqueados, subcilíndricos ou aciculares, com 1–7 septos transversais, de 15–37 × 2.5 μm ...', this may well be a facultative synonym of *Leptorhaphis oleae* Massal. (p. 00), which also grows on the bark of olive trees in the Mediterranean region. Until conclusive evidence of this is obtained, it does, however, seem prudent to treat the taxon as of uncertain position. A third species has been described on olive tree bark, *L. michaudii* B. de Lesd., but according to the description the taxon has globose ascomata instead of dimidiate, and occasionally semicircular ascospores.

Leptorhaphis patzaltii Poetsch *in* Poetsch & Schiedermayr, *Syst. Aufz. Erzh. Oest. Pfl.* (Krypt.): 180 (1872). Type: Austria, Oberösterreich, Kremsmünster, Pestleitenholz, 'auf *Graphis serpentina* an Ahornstämmen' with *Arthopyrenia microspila* Körber [i.e. *Stigmidium microspilum* (Körber) D. Hawksworth].

OBSERVATIONS. This epithet was not validly published according to Art. 32.1, and no material was available from W. B. Keissler (1938: 266) mentioned that Poetsch's herbaria could be found both at Seitestetten (Niederösterreich) and Kremsmünster (Oberösterreich), but material was not located there either.

Lahmia piceae Anzi ex Rehm, *Rabenh. Krypt., Fl.* **1**, 2(3): 343 (1896). *Lahmia piceae* Anzi, *Lich. langob. min. rar. exs.* no. 457 (1866); nom. inval. (Art.32.1.). *Lahmiomyces piceae* (Anzi) Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittogam. Pavia* V, **10**: 270 (1953). Type: Italy, Valfurva, Valdidentro, near Bormium, on bark of *Pinus picea* [Anzi, *Lich. Lang. exs.* no. 457] (BM!—isotype).

Lahmia kunzei var. *ecrustacea* Anzi, *Comment. Soc. crittogam, Ital.* **2**: 22 (1864); nom. inval. (Art.32.1.).

Fig. 69B, 70.

OBSERVATIONS. Type material of this species from BM was misidentified as *Leptorhaphis lucida* Lahm, presumably for the same reasons used by Vainio (1921: 188) to refer to *Lahmia kunzei* Körber as *Leptorhaphis lucida*. However, both species are not closely related because they have a very different ascomatal structure. The asci are typically clavate in *Lahmia piceae*, very thin at the base, and the ascospores are shorter (35–45 × 2–3.5 μm), and usually 3-septate. This species also lacks the characteristic pseudoparaphyses always present in the genus *Leptorhaphis*. Although the anatomy of the ascomatal wall resembles that in *Lahmia kunzei*, it differs from the latter in the arrangement of asci and paraphysoids in the hymenium, which is covered by a thin epithecium, formed by the tips of the paraphysoids. These become free, branched and slightly capitate, as in the Lecanidion type of development (Eriksson, 1981: 79). This has already been pointed out by Eriksson (1986: 356), who placed *Lahmia piceae* Anzi ex Rehm (as *Lahmiomyces piceae* (Anzi ex Rehm) Cif. & Tom.) in the Patellariaceae, and proposed the new family Lahmiaceae and the new order Lahmiales to accomodate the genus *Lahmia* Körber and its type species *Lahmia kunzei*.

Campylacia quercus Beltram., *Lich. Bass.*: 250 (1858). *Leptorhaphis quercus* (Beltram.) Körber, *Parerg. lich.*: 385 (1865). *Spermatodium quercus* (Beltram.) Trevisan, *Consp. verruc.*: 12 (1860). *Verrucaria quercus* (Beltram.) Nyl. in *Flora, Jena* **58**: 14 (1857). Type: Italy, Vicenza, Bassamo d'Grappa, S. Michiele wood, on young oaks.

OBSERVATIONS. Type material of this taxon was requested from PAD, where Beltramini's herbarium is now kept, but

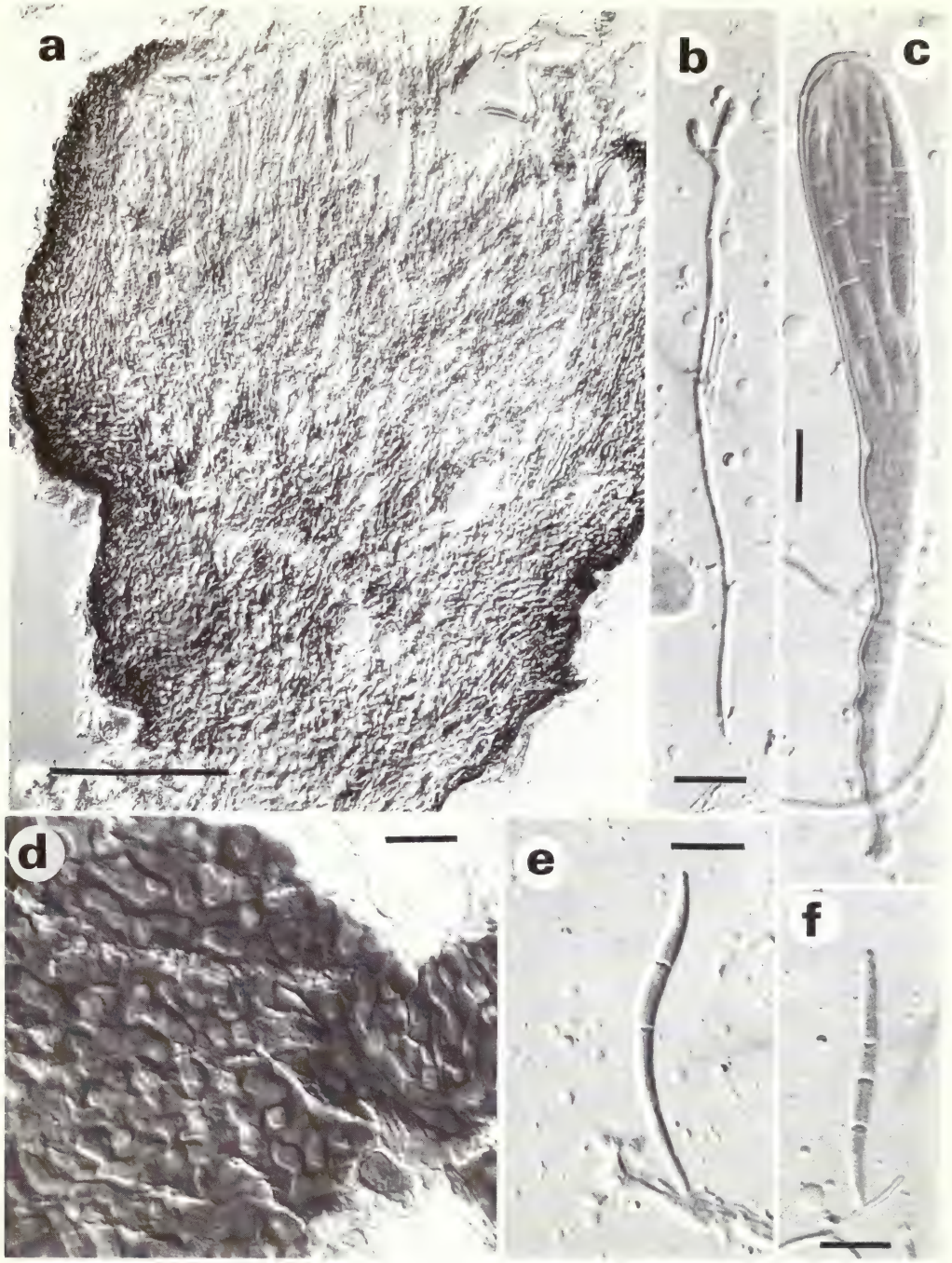


Fig. 70 *Lahmiomyces piceae* (Anzi) Cif. & Tom. (BM–isotype of *Lahmia piceae*) (a) Section of ascoma; scale = 100 μm; (b) Paraphyses, capitate and apically branching; (c) Ascus and ascospores; (d) Detail of exciple: textura intricata; (e), (f) Ascospores; scale = 10 μm.

the specimens filed as *Leptorhaphis quercus* did not agree with the description and illustrations prepared by the author in 1858, except for one specimen, on *Corylus* bark, which I identified as *Leptorhaphis maggiana* (Massal.) Körber. Beltramini (1858: 250) described a fungus with very small and punctiform, spherical, and scattered 'apothecia', with asci presumably bitunicate in structure, and with long and narrow ascospores, 1- to 3-septate, which he regarded as differing from *Campylacia maggiana* Massal. [syn. *Leptorhaphis maggiana* (Massal.) Körber] in its three or four times bigger ascomata. Keissler (1938: 241) considered Arnold's exsiccate no. 1510 on oak bark, the second specimen in PAD, to be *Leptorhaphis quercus*, whereas he referred a third specimen at PAD [Zahlbruchkner, *Lich. rar. exs.* no. 131] to *L. quercus* f. *macrospora* [i.e. *Cresporhaphis macrospora* (Eitner) Aguirre]. I agree with the latter opinion, but Arnold's exsiccate should be referred to the genus *Rhaphidicyrtis*, as *R. trichosporella* (Nyl.) Vainio, which clearly differs from the

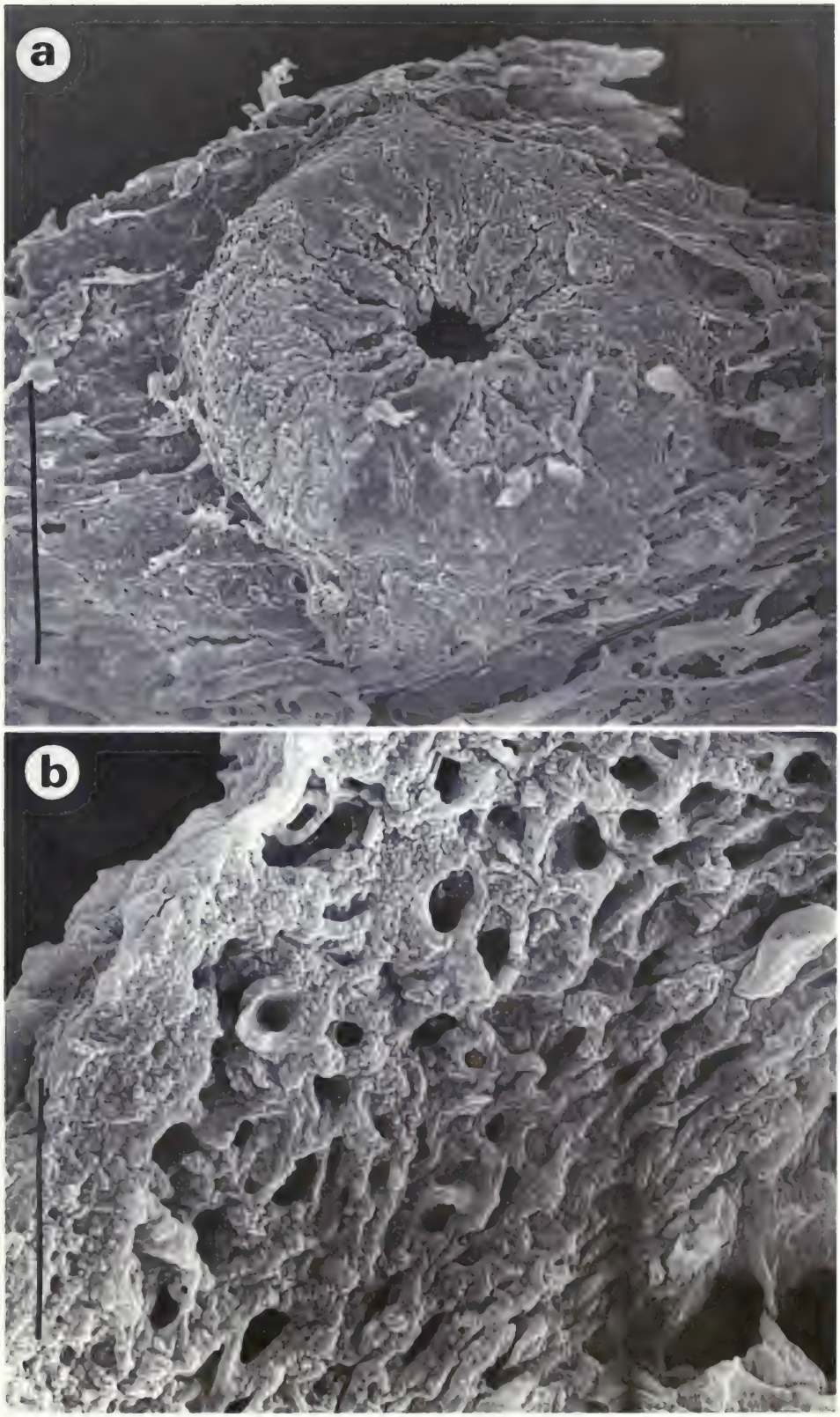


Fig. 71 *Odontura rhaphidospora* (Rehm) Clem. (S–lectotype of *Leptorhaphis pyrenopezizoides*) (a) Surface view of ascoma; scale = 176 µm; (b) Detail of exciple: pseudoparenchymatous tissue of leptodermatous cells in places, not neat textura angularis; scale = 8.6 µm.

species represented and described by Beltramini in ascomatal structure, ascus and ascospore morphology, and size.

At present this taxon is retained as an excluded species until new evidence or the type material is located. Material was also requested from BASSA but without success.

Pyrenopeziza rhaphidospora Rehm in *Ber. naturhist. Ver. Augsburg* 26: 75 (1881). *Beloniella rhaphidospora* (Rehm) Boud. in *Bull. Soc. mycol. Fr.* **1**: 119 (1885). *Odontotrema rhaphidosporum* (Rehm) Rehm, *Rabenh. Krypt., Fl.*, **1**(3): 207 (1888). *Belonium rhaphidosporum* (Rehm) Sacc., *Syll. Fung.* **8**: 495 (1889). *Odontura rhaphidospora* (Rehm) Clem. *Gen. Fungi*: 174 (1909). *Odontotremella rhaphidospora* (Rehm) Rehm in *Ber. bayer. bot. Ges.* **13**: 166 (1912). Type: Austria, Tyrol, Oetz, Kühtei, Längenthal, *c.* 2100 m, on decaying wood of *Pinus cembra*, August 1874, *H. Rehm* [Rehm, *Ascomyceten exs.* no. 298 as *Leptorhaphis pyrenopezizoides*] (S!—lectotype; K!, E!—isolectotypes).

Leptorhaphis pyrenopezizoides Rehm, *Ascomyceten exs.* no. 298 (1875); nom. inval. (Art. 32.1).

Ramonia athalina Sherw. in *Mycotaxon* **6**: 186 (1977). Type: Bulgaria, Pirin Mountains,'sub hospitem Vichrem', 1000 m,'ad lignum *Pini peuce*', August 1966, *A. Vèzda* (CUP 55860!—holotype).

Fig. 71, 72.

Thallus: Immersed in wood, consisting of colourless, undulating, thin-walled, smooth, cylindrical and septate hyphae, 2–3.5 µm wide, constricted at the septa and dichotomously branched, which become dark brown towards the surface, sometimes associated with trebouxoid algae, 3–8 µm cells diam, which could also be found below the hymenium.

Ascomata: Circular, black, matt, not pruinose, radially furrowed from the pore, which is centrally located, scattered singly and sometimes confluent, individual ascomata 500–800 µm diam; globose, becoming deeply urceolate, immersed in the wood to half of its height and opening by a dentate pore. Exciple: dark brown, covering the centrum except at its base in young ascomata, becoming marginal and composed of two colour layers, lacking crystalline inclusions, the outer wall dark brown to nearly black, 20–35 µm thick, incorporating substratum material in its lower part, the inner wall colourless and thinner, *c.* 20 µm thick, leading to a layer of periphysoids; both layers composed of more or less isodiametric, thick-walled cells of small lumen, 2–4 µm diam, forming a pseudoparenchymatous tissue. Hamathecium: of paraphyses, composed of colourless, smooth, thin-walled hyphae, about 1 µm wide, sparsely septate, the apical cell capitate, free at the apex, arising from the base of the ascoma; periphysoids, colourless, unbranched, *c.* 1.5 µm wide, composed of a few cells, thin-walled, the apical cell always capitate, in young ascomata clearly growing downwards, but becoming and remaining marginal in expanded ascomata; hymenial gelatin not changing colour in iodine. Asci: arising from the base of the ascoma, ripening sequentially, cylindrical-clavate, short-stalked, 60–75 × 15 µm, single layered, thin-walled, apex not turning blue in iodine; no apical structures seen; more than 8-spored; opened asci not observed. Ascospores: colourless, thin-walled, smooth, filiform and multiseptate when mature, breaking up and producing 1-septate and fusiform part-spores, 16–30 × 1.5–2 µm; arranged in a fascicle, sometimes twisted helically; full size ascospores not observed free.

Conidiomata: Not observed.

ECOLOGY. On decorticate conifer wood, not causing any apparent damage; probably saprophytic, although sometimes, and especially in fresh collections, the mycelium is associated with green algae.

DISTRIBUTION. Described from the Tirol (Austria), this fungus is also known in Europe from Switzerland (Ticino and Valais), Bulgaria (Pirin Mountains), and Sweden (Sherwood-Pike, 1987); and from Norway according to Holm & Holm (1977), but I have not studied material from the latter two countries. It is evidently widely distributed in Scandinavia and the mountains of central Europe (Sherwood-Pike, 1987).

TYPIFICATION. Material under the name *Leptorhaphis pyrenopezizoides* was distributed in an exsiccate by Rehm (1875), but without a proper description; thus according to Art. 32.1 the name was not validly published then. Later, Rehm (1881: 75) changed his opinion as to the identity of the species, and described the new taxon *Pyrenopeziza rhaphidospora* (sub *Leptorhaphis pyrenopezizoides*) based on the exsiccate previously distributed. No holotype was selected, nor have other authors indicated a lectotype. The specimen in Rehm's exsiccate, in his herbarium at S, is here designated as the lectotype.

OBSERVATIONS. This taxon is currently accepted as *Odontura rhaphidospora* (Rehm) Clem. in the family Odontotremataceae D. Hawksw. & Sherw. (1982), together with other ostropalean fungi with hemiangiocarpic, apothecioid ascomata, simple paraphyses, and cylindrical, and I–asci, such as *Odontotrema*, *Skyttea* etc.; for a more detailed description and discussion of the systematic position of this fungus see Sherwood (1977*b*, 1987), and Müller & Défago (1966). Sherwood et al. (1980), and Coppins (1987) in a recent account of the British species of the genus *Ramonia* mentioned that *Ramonia athalina* Sherw., was a synonym of *Odontura rhaphidospora*, and can be excluded from *Ramonia* in the structure of the exciple, which has a neat textura angularis (see Fig. 71 and Coppins, 1987: Fig. 2B).

ADDITIONAL SPECIMENS. **Switzerland**, Valais, Brig, Aletschreservat, Kt. Wallis, on wood of *Pinus cembra*, 13 June 1963, *E. Müller* (K). Ticino, Airolo, Val Piora, South shore of Lago Ritom, Larici di Campo, SW Mottone, *c.* 1800 m, 'im Lärchen-Erlen-Wald', 30 August 1984, *G. Rambold & D. Triebel* (M–G. Ramb. 2663 & D. Triebel 556).

Leptorhaphis steinii Körber ex Stein *in* Cohn, *Krypt., Fl. Schles.* **2**(2): 349 (1879). *Leptorhaphis steinii* Körber *in* Stein *in Jber. schles. Ges. vaterl. Kult.*: 139 (1869); nom. inval. (Art. 32.1). *Leptosphaeria steinii* (Körber) Winter, *Rabenh. Krypt., Fl.* **1**(2): 443 (1885). *Ophiobolus steinii* (Körber) Berl. & Vogl. *in* Sacc., *Syll. Fung., Additamenta ad volumina* I–IV: 189 (1886). *Metasphaeria steinii* (Körber) Schröter *in* Cohn, *Krypt., Fl. Schles.* **3**(2): 355 (1894). Type: Poland, Silesia,'Basalt der kleinen Schnegrusse', on *Porpidia glaucophaea*, 1870?, *B. Stein* (WRSL!—isolectotype).

Fig. 73, 74A.

Thallus: Absent.

Ascomata: Perithecioid, black and brittle (carbonaceous), shiny, smooth, scattered singly, 400–600 µm diam; completely immersed in the substratum, somewhat spherical, opening

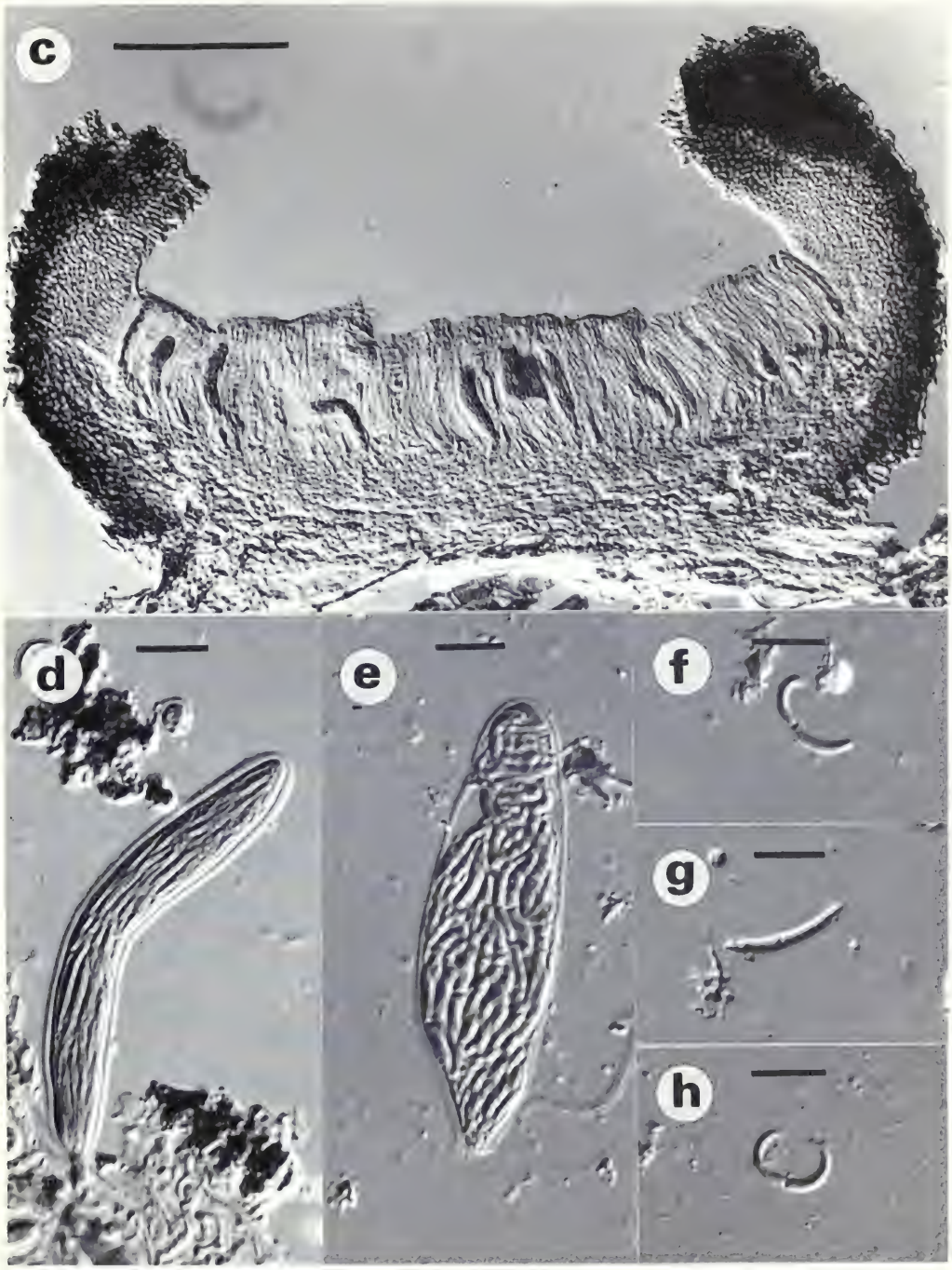


Fig. 72 *Odontura rhapidospora* (Rehm) Clem. (S–lectotype) (c) Vertical section of ascoma, showing marginal layer of periphysoids; scale = 100 μm; (d) Ascus and ascospores; (e) Ascus and part-ascospores; (f), (g), (h) Part-ascospores; scale = 10 μm.

through a central ostiole, *c.* 10 μm wide. *Wall*: dark brown, nearly black, 35–55 μm thick, becoming thicker at the sides near the surface, 100–150 μm thick; composed of isodiametric, thick-walled cells, *c.* 4 μm diam, with brown walls and small lumina, forming a pseudoparnchymatous tissue of mesodermatous cells, reminiscent of a textura globulosa, becoming a textura porrecta in places; sometimes incorporating crystalline inclusions at the base and sides. Hamathecium: of paraphysoids, composed of colourless, smooth and narrow hyphae, *c.* 1–1.5 μm wide, infrequently septate, anastomosing, not constricted at the septa, surrounded by mucus; periphyses also present, composed of colourless, smooth, thin-walled hyphae, *c.* 1–1.5 μm wide, infrequently septate, not constricted at the septa; hymenial gelatin bluish-green in iodine. Asci: arising from the base of the ascomatal cavity, ripening sequentially, cylindrical-clavate, 70–90 × 10–12 μm, long-stalked, apparently bitunicate, with a very thin and smooth outer wall, almost inapparent, inner wall with a

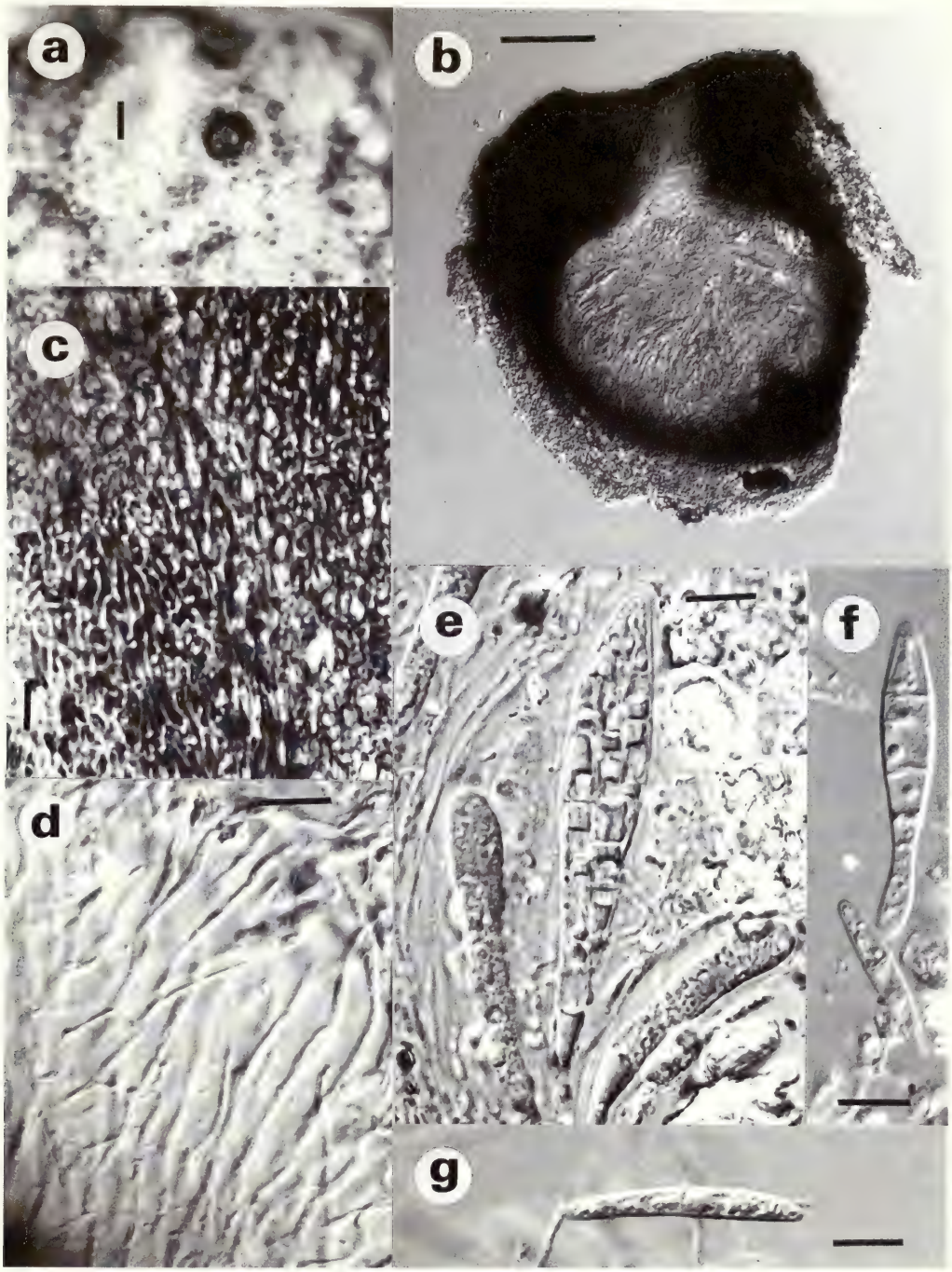


Fig. 73 *Sagediopsis barbara* (Th. Fr.) R. Sant & D. Triebel (WRSL–isolectotype of *Leptorhaphis steinii*) (a) Surface view of ascoma; scale = 500 µm; (b) Vertical section of ascoma; scale = 100 µm; (c) Detail of exciple: textura angularis and porrecta; (d) Periphyses in ostiolar channel; (e) Asci and ascospores; (f), (g) Ascospores; scale = 10 µm.

short internal apical beak, not staining in iodine; no other apical structures seen; 8-spored; opened asci not observed. Ascospores: colourless to yellowish, with thin brownish walls, smooth, fusiform, 30–45 (-55) × 3–4.5 µm, 3- to 5-septate, not constricted at the septa, each cells containing few large refringent particles, without appendages or conidiogenous sheaths.

Conidiomata: Not observed.

ECOLOGY. This species has a lichenicolous habit, growing on the thallus of *Porpidia glaucophaea* (Körber) Hertel & Knoph on siliceous rocks; it does not discolour or cause any apparent damage to the host lichen thallus and is presumably commensalistic.

DISTRIBUTION. Europe, known from central Europe (Poland, Silesia) and Scandinavia (Sweden and Norway), principally in montane regions with siliceous rocks.

TYPIFICATION. *Leptorhaphis steinii* was lectotypified by Triebel (1989: 110), and this is fully accepted here.

OBSERVATIONS. The lichenicolous habit of the species immediately suggests that it is not related to *Leptorhaphis* Körber s. str., which as defined here only includes saprophytic and loosely lichenized species. The ascomata and hamathecial structures differ from those of *Leptorhaphis*, as well as the morphology of the asci and ascospores. Keissler (1938: 267) recognized that this was a lichenicolous species and referred it to *Ophiobolus* as *O. barbarus* (Th. Fr.) Keissler. Fries (1867: 108) described this as *Segestria barbara*, also pointing out that its systematic position was not yet clear, and that perhaps it was related to the genus *Leptorhaphis*. Recently R. Santesson and D. Triebel (Triebel, 1989: 110–115) studied carefully the type material of both taxa, concluding that both are synonyms and that they should be referred to the genus *Sagediopsis* (Sacc.) Vainio (1921: 191) as *S. barbara* (Th. Fr.) R. Sant & Triebel, which was erected to accommodate the single lichenicolous fungus *Verrucaria tartarina* Nyl. [i.e. *Sagediopsis tartarina* (Nyl.) Vainio], with fusiform, 3-septate ascospores growing on thalli of *Ochrolechia tartarea* (L.) Massal.

ADDITIONAL SPECIMENS. **Norway**, Akershus, Oslo, Ekeberg, September 1867, *N. G. Moe* (W II & 163). **Poland**, Silesia, 1 September 1872, *B. Stein* [Körber, *Lich. Sel. Germ. exs.* no. 325, as *Leptorhaphis steinii*] (WRSL, W II/163); loc. cit., *G. W. Körber* [Körber, *Lich. Sel. Germ. exs.* no. 325, as *L. steinii*] (BP); loc. cit., 1865, *B. Stein* (WRSL). **Sweden**, Kopparberg Falun,'Dalarna, Fahlun', on *Lecidea contigua* [i.e. *Porpidia glaucophaea*], 1867, *P. De Laval* (UPS—holotype of *Segestria barbara*).

Arthopyrenia stenomicra Norman in *Ofvers. K. VetenskAkad. Förh. Stockh.* **41**(8): 39 (1884). *Leptorhaphis stenomicra* (Norman) Magnusson in *Förteckn. Skandinaviens växter* **4**: 11 (1956). Type: Norway, Vestfold, Larvik, Sky, 'fraxinicola', *J. M. Norman* (UPS!—holotype).

Fig. 75.

OBSERVATIONS. The holotype of this taxon was located in UPS, but despite a careful study of the specimen, I failed to find ascospores with the characteristics described in the protologue. Instead, I found an *Arthonia* species (see Fig.75), together with an anamorph, in those areas on the specimen where Norman outlined as having the species. I was unable to observe conidia, but did see conidiogenous cells, which were colourless, lageniform, thick-walled, and *c.* 6 µm in length. The size of the conidiomata, *c.* 60 µm diam, is about the same as that described by Norman (1884) for the'ascomata' of the species, but there is no proof that this pycnidial state belongs to any *Arthopyrenia* species, and vice versa.

Lichen sticticus Ach., *Lich. suec. Prod.*: 16 (1798). *Verrucaria stictica* (Ach.) Ach., *Meth. Lich.*: 118 (1803). *Verrucaria byssacea* var. *stictica* (Ach.) Ach., *Lich. Univ.*: 294 (1810). *Cyphelium sticticum* (Ach.) Ach. in *K. svenska VetenskAkad. Handl.* **1** 269 (1815). *Limboria stictica* (Ach.) Ach. in *K. svenska VetenskAkad. Handl.* **3**: 223 (1817). *Pyrenothea stictica* (Ach.) Th. Fr., *Lich. Eur.*: 452 (1831). Type: Sweden, on *Salix* (H–ACH 452!—holotype).

Fig. 74B, 76.

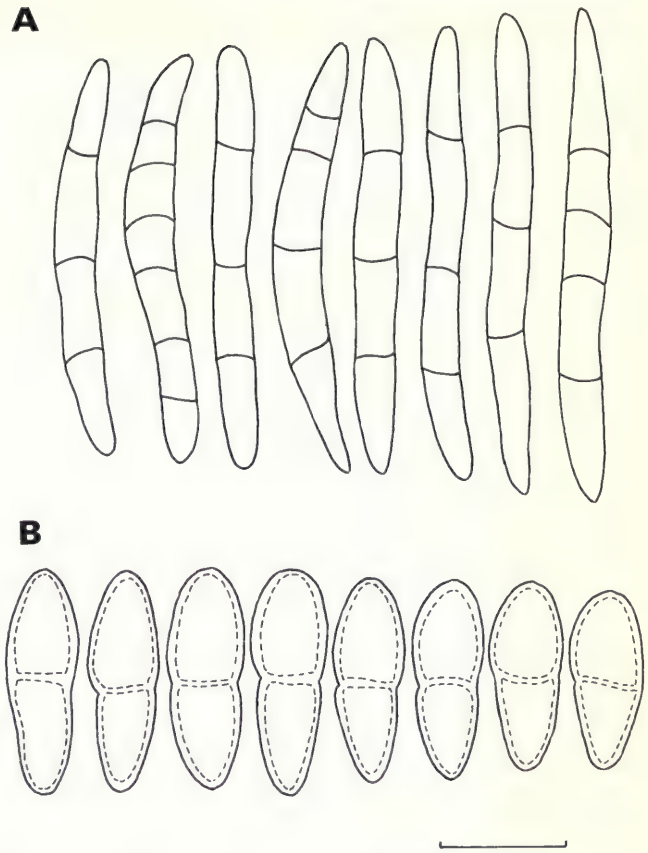


Fig. 74 Ascospore outlines (A) *Sagediopsis barbara* (Th. Fr.) R. Sant & D. Triebel (WRSL–isolectotype of *Leptorhaphis steinii*); (B) *Lichen sticticus* Ach. (H–ACH 452–holotype); scale = 10 µm.

OBSERVATIONS. The collection of *Lichen sticticus* in the Acharius herbarium in Helsinki contains a mixture of pieces of bark from different localities. According to the protologue, the specimen named as 'Suecia, *Salix*' should be the holotype, but this differs from a putative isotype in BM-ACH 311. Thus the former is an *Arthopyrenia*-like species, closely related to *A. lapponina* Anzi in the structure of the ascomata, ascus and ascospore morphology, and size (Harris, 1975), whilst the latter is a species referable to the genus *Cresporhaphis*, as *C. wienkampii* (Lahm ex Hazslin) Aguirre (p. 154). Zahlbruckner (1922: 345) placed *Verrucaria stictica* Sommerfelt (not Acharius) as a synonym of *Leptorhaphis tremulae*, probably following a recommendation made by Th. Fries (1860: 374). However, Sommerfelt (1826) did not intend to describe a new species but applied Acharius' name. Therefore the species should be typified by Acharius' name, and referred to the genus *Arthopyrenia* Massal.

Verrucaria punctiformis var. straminea Eschw. *in* Martius, *Flora Brasiliensis ordo secundus-Lichenes*: 124 (1833). *Verrucaria straminea* (Eschw.) Krepelh. in *Vidensk. Meddr. danks naturh. Foren.* **5**: 33, tab. I, fig. 25 (1873). *Arthopyrenia straminea* (Eschw.) Müll. Arg. in *Flora, Jena* **66**: 319 (1883). *Leptorhaphis straminea* (Eschw.) Zahlbr., *Cat. lich. univ.* **1**: 344 (1922). Type: Brazil, Brasilia Province, Pará,'ad corticem arborum', *C.F.P. Martius* (M!—2 isotypes).

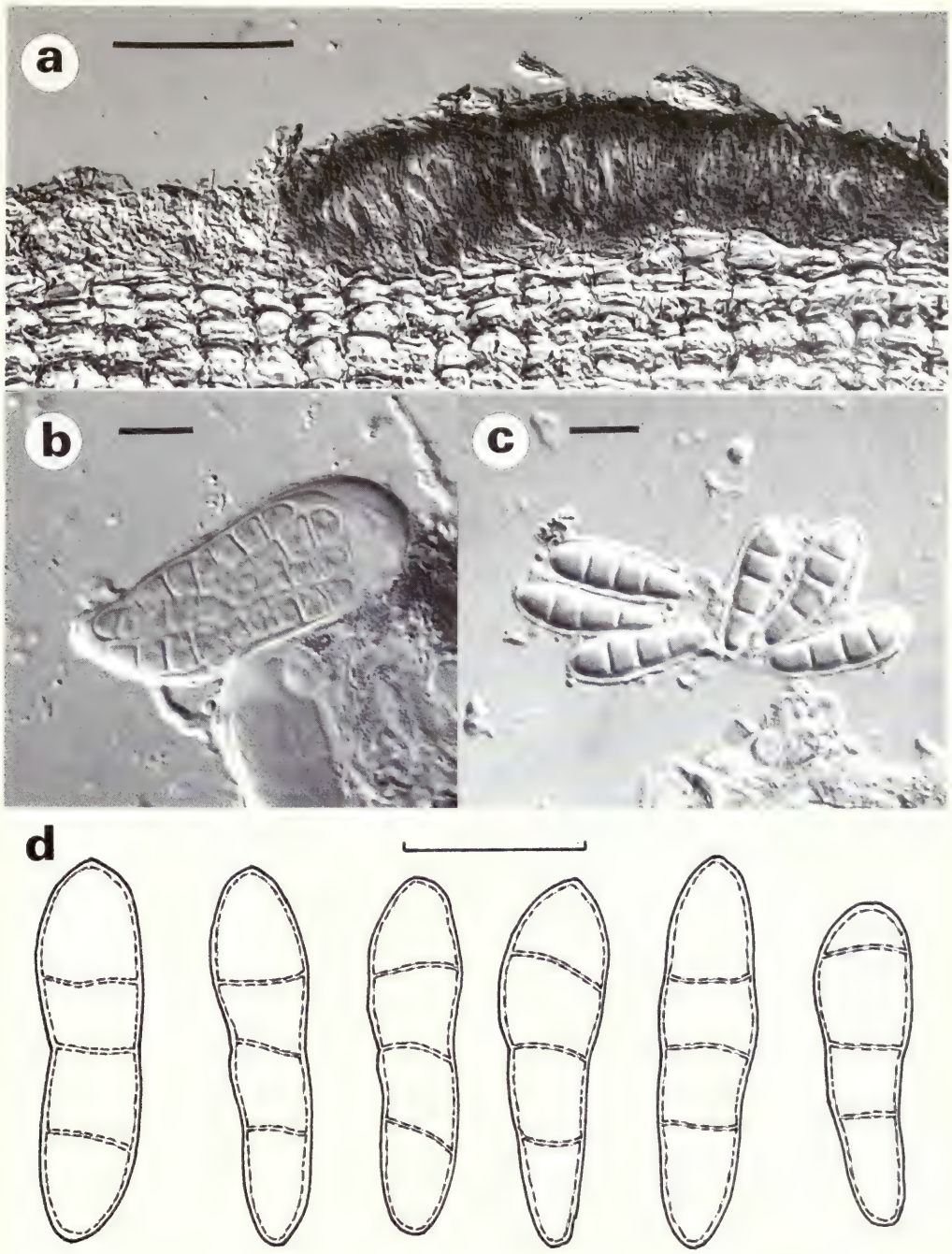


Fig. 75 *'Leptorhaphis' stenomicra* Norman (UPS–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Ascus and ascospores; (c) Ascospores; (d) Ascospore outlines; scale = 10 μm.

OBSERVATIONS. Two isotypes of this species have been kept at M herbarium, but after a careful study of the material, I was unable to observe asci, ascospores, or any other structure except for the black and brittle involucrellum of the ascomata, which structurally differs from the involucrellum of *Leptorhaphis*, and it is reminiscent of those of the Pyrenulales. The material is probably lichenized, associated with chlorococcoid algae. In the original description, Eschweiler (1833) did not provide information on ascospore morphology and size, whilst Krempelhuber (1873) described a corticolous fungus with fusiform colourless to olivaceous, thick-walled ascospores, 3- to 5-septate, from Brazil (Lagoa Santa). On the basis of the ascomatal structure and ascospore characteristics the species must be excluded from *Leptorhaphis*, and it is tentatively placed within the Pyrenulales.

ACKNOWLEDGEMENTS. I am indebted to Professor D. L. Hawksworth, who proposed the topic, for guidance and constructive criticism throughout, and in making the facilities of the CAB International Mycological Institute (Kew) available during and after my thesis

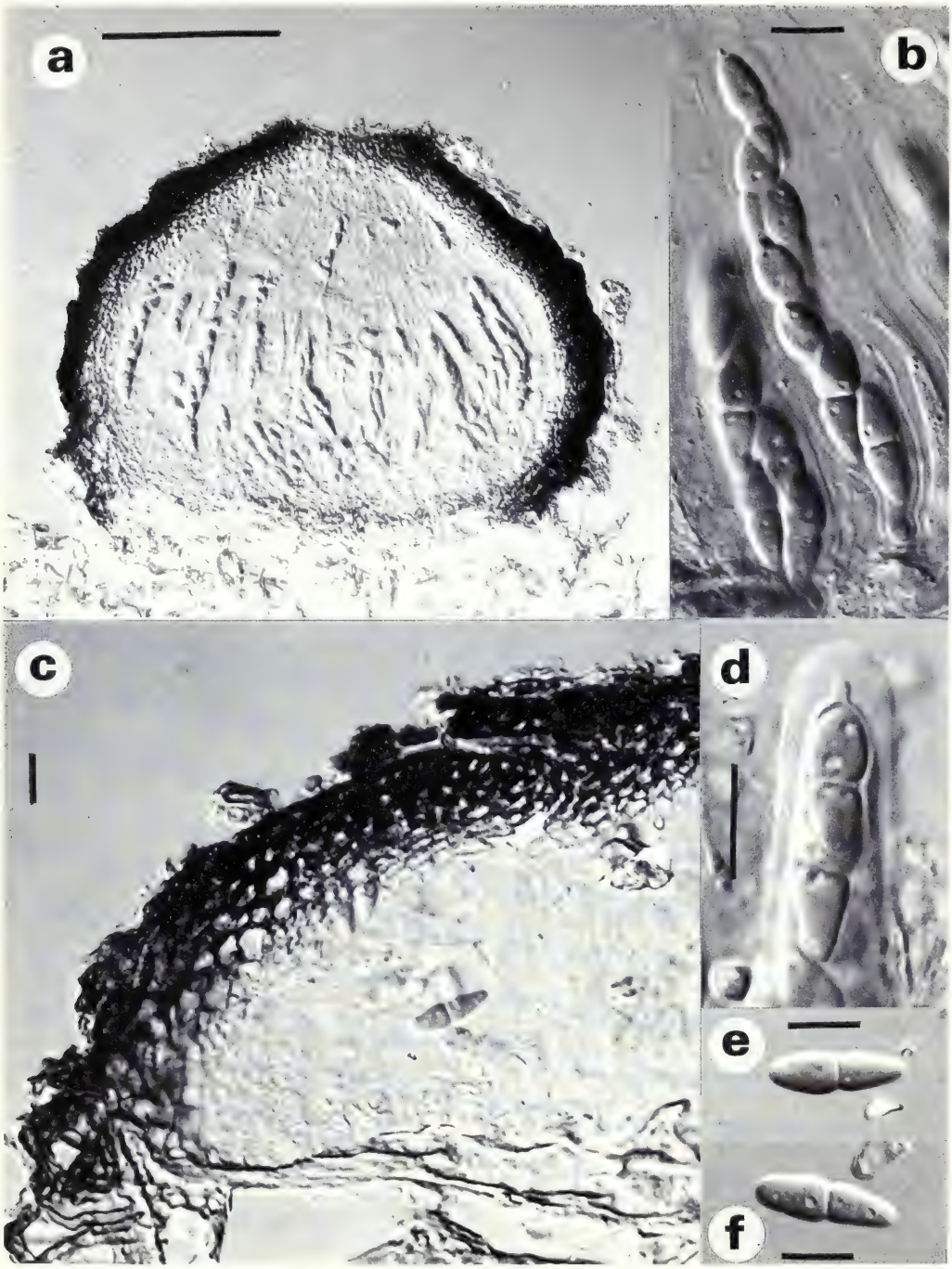


Fig. 76 *Lichen sticticus* Ach. (H-ACH 452–holotype) (a) Vertical section of ascoma; scale = 100 μm; (b) Ascus and ascospores; (c) Detail of exciple: textura angularis; (e), (f) Ascospores; scale = 10 μm.

work; and to the directors and curators of the following institutional herbaria from which I borrowed material : B, BM, BP, C, Concarneau, CUP, E, G, H, K, L, LD, LISU, M, O, PAD, PC, S, TNC, TUR, UPS, VER, W, WELT, WRSL, with especial thanks to P. W. James, O. Vitikainen, H. Krog, H. Sipman, R. Moberg, E. S. Hansen, B. C. Coppins, and G. Degelius. Also, I would like to thank Dr M. R. D. Seaward for his help in obtaining the material from WRSL, and assistance in 'translating' the information on packets; Mme Locquin (PC), and The Director of the Laboratoire de Biologie Marine du Collège de France (CNRS) (Concarneau) for their hospitality during visits there; Miss D. Triebel for her help with the identity of '*Leptorhaphis' steinii*; Mr J. R. Laundon for his help with some nomenclature and final editing of the manuscript; and the referees, Drs R. C. Harris and E. Sérusiaux, for their helpful comments.

Drs D. W. Minter, A. Sivanesan, and O. Eriksson are acknowledged for valuable and stimulating taxonomic discussions, as well as Roz Lowen and Andrea Romero for their companionship on several occasions.

My husband, Kenneth Hudson, assisted with bibliographic work,

preparing drawings, word-processing, and checking of the manuscript. Miss G. F. Godwin is thanked for photographic assistance, and Mrs U. Hawksworth for correcting the Latin description of the new genus.

Finally, Hezkuntza, Unibertsitate eta Ikerketa Saila, Eusko Jaularitza [Department of Education, Universities and Research, Basque Goverment], Gasteiz, Spain, is acknowledged for financial support over the study period.

REFERENCES

Aguirre, B, & Hawksworth, D. L. 1987. The circumscription, biology and relationships of the genus *Leptorhaphis* Körber. *In* E. Peveling (Ed.) *Progress and problems in lichenology in the eighties. Bibl. lichenol.* **25**: 249–253. Berlin.

Ahmadjian, V. 1974 ['1973']. Methods in isolating and culturing lichen symbionts and thalli. *In* V. Ahmadjian & M. E. Hale (Eds) *The Lichens*: 653–659. London.

Arx, J. A. von & Müller, E. 1975. A re-evaluation of the bitunicate ascomycetes with keys to families and genera. *Stud. Mycol.* **9**: 1–159.

Awasthi, D. D. & Agarwal, M. R. 1968. New or otherwise interesting lichens from Darjeeling District, India. *Can. J. Bot.* **46**: 1025–1030.

Baral, H. O. 1987. Lugol's solution/IKI versus Melzer's reagent: hemiamyloidity, a universal feature of the ascus wall. *Mycotaxon* **29**: 399–450.

Barr, M. E. 1977. *Acanthostigmella* (Herpotrichiellaceae). *Mycotaxon* **6**: 17–23.

—— 1979. A classification of Loculoascomycetes. *Mycologia* **71**: 935–957.

—— 1983. The ascomycete connection. *Mycologia* **75**: 1–13.

Beltramini de Cesati, F. 1858. *I lichenis Bassanesi enumerati e descritti*. Bassano.

Booth, C. 1958. The genera *Chaetosphaeria* and *Thaxteria* in Britain. *Naturalist, Hull*: 83–90.

—— 1971. Introduction to general methods. *In* C. Booth (Ed.) *Methods in microbiology* **4**: 1–47. London.

Bouly de Lesdain, M. 1907. Lichens des environs d'Hyères (Var): recueillis par M. C. Michaud. *Feuille jeun. Nat.* IV, **37**: 66–71.

Bowler, P. A. & Rundel, P. W. 1975. Reproductive strategies in lichens. *Bot. J. Linn. Soc.* **70**: 325–340.

Cannon, P. F., Hawksworth, D. L. & Sherwood-Pike, M. A. 1985 *The British Ascomycotina: an annotated checklist*. Slough.

Chadefaud, M. 1973. Les asques et la systématique des Ascomycètes. *Bull. Soc. mycol. Fr.* **89**: 127–170.

Chesters, C. G. C. 1938. Studies on British Pyrenomycetes II: A comparative study of *Melanomma pulvis-pyrus* (Pers.) Fuckel, *Melanomma fuscidulum* Sacc. and *Thyridaria rubro-notata* (B. & Br.) Sacc. *Trans. Br. mycol. Soc.* **22**: 116–150.

Ciferri, R. & Tomaselli, R. 1953. Saggio di una sistematica micolichenologica. *Atti Ist. bot. Univ. Lab. crittog. Pavia* V, **10**: 25–84.

Clauzade, G. & Roux, C. 1985. *Likenoj de Okcidenta Eûropo. Ilustrita determinlibro*. Royan-France.

Clements, F. E. 1909. *The genera of Fungi*. Minneapolis.

—— **& Shear, C. L.** 1931. *The Genera of Fungi*. New York.

Cohn, F. J. 1879. *Kryptogamen-Flora von Schlesien* **2**(2). Breslau.

Cole, G. T. & Samson, R. A. 1979. *Patterns of development in conidial fungi*. London.

Coppins, B. J. 1983. A taxonomic study of the lichen genus *Micarea* in Europe. *Bull. Br. Mus. nat. Hist.* (Bot.) **11**: 17–214.

—— 1987. The genus *Ramonia* in the British Isles. *Lichenologist* **19**: 409–417.

—— 1988. Notes on the genus *Arthopyrenia* in the British Isles. *Lichenologist* **20**: 305–325.

Crouan, H. M. & Crouan, P. L. 1867. *Florule du Finistère*. Paris.

David, J. C. 1986. A survey of taxonomic concepts in the ascomycete microfungi with reference to the taxonomy of the genus *Stigmidium* Trevisan. MSc thesis: University of Reading.

Degelius, G. 1942. The lichen flora of North America. *Ark. Bot.* **30**: 1–62.

Dring, D. M. 1971. Techniques for microscopic preparation. *In* C. Booth (Ed.) *Methods in microbiology* **4**: 95–111. London.

Eriksson, O. 1967. On graminicolous pyrenomycetes from Fennoscandia, 1. Dictyosporous species. *Ark. Bot.* II, **6**: 339–379.

—— 1981. The families of bitunicate ascomycetes. *Op. bot.* **60**: 1–220.

—— 1986. *Lahmia* Körber (= *Parkerella* A. Funk) a misinterpreted genus with isolated position. *Mycotaxon* **27**: 347–360.

—— **& Hawksworth, D. L.** 1986. Outline of the ascomycetes-1986. *Systema Ascomycetum* **5**: 185–324.

—— **& Hawksworth, D. L.** 1987*a*. An alphabetical list of the generic names of the Ascomycetes. *Systema Ascomycetum* **6**: 1–109.

—— **& Hawksworth, D. L.** 1987*b*. Notes on ascomycete systematics, 464–551. *Systema Ascomycetum* **6**: 237–258.

—— **& Hawksworth, D. L.** 1987*c*. Outline of the ascomycetes-1987. *Systema Ascomycetum* **6**: 259–338.

—— **& Santesson, R.** 1986. *Lasiosphaeropsis stereocaulicola*. *Mycotaxon* **25**: 569–580.

Eschweiler, F. G. 1833. Ordo secundus lichenes. *In* C. F. P. Martius, *Flora Brasiliensis* **1**: 51–293. Tubingae.

Farr, E. R., Leussink, J. A. & Stafleu, F. A. (Eds) 1979. *Index nominum genericorum (Plantarum)*. [Regnum veg. **100–102**] Utrecht.

Fée, A. L. 1837. *Essai sur les Cryptogames des écorces exotiques officinales* II. *Supplément et révision*. Paris.

Fink, B. 1910. The lichens of Minnesota. *Contr. US natn. Herb.* **14**(1): 1–269.

Fries, Th. M. 1860 ['1861']. Lichenes arctoi Europae groenlandiaeque hactemus cogniti collegit examinavit disposuit. *Nova Acta R. Soc. Scient. upsal.* III, **3**: 103–398.

—— 1861. *Genera heterolichenum europaea recognita*. Uppsala.

—— 1867. 2. Nya Skandinaviska laf-arter. *Bot. Notiser*: 151–155.

Funk, A. & Zalasky, H. 1974. *Rhytidiella baranyayi* n.sp., associated with cork-bark of aspen. *Can. J. Bot.* **53**: 752–755.

Galloway, D. J. 1985. *Flora of New Zealand. Lichens*. Wellington.

Gams, W. & Holubová-Jecková, V. 1976. *Chloridium* and some other dematiaceous hyphomycetes growing on decaying wood. *Stud. Mycol.* **13**: 1–99.

Garovaglio, S. 1865. *Tentamen dispositionis methodicae lichenum in Longobardia nascentium* **2**: *Verruc. bilol. ill.* Medioli.

Goebel, K. C. T. Fr. & Kunze, G. 1827–1829. Enthaltend die Rinde und ihre Parasiten aus der Ordnung der Flechten, VIII. *Pharmaceutische Waarenkunde* **1**(1/6). Eisenach.

Hafellner, J. 1979. *Karschia*. Revision einer Sammelgattung an der Grenze von lichenisierten und nichtlichenisierten Ascomyceten. *Beih. Nova Hedwigia* **62**: 1–248.

Harris, R. C. 1973. The corticolous pyrenolichens of the Great Lakes region. *Michigan botanist* **12**: 3–68.

—— 1975. *A taxonomic revision of the genus* Arthopyrenia *Massal.* s. lat. *(Ascomycetes) in North America*. PhD thesis: Michigan State University.

—— 1989. A sketch of the family Pyrenulaceae (Melanommatales) in eastern North America. *Memoirs of the New York Botanical Garden* **49**: 74–107.

Hawksworth, D. L. 1974. *Mycologist's handbook*. Kew.

—— 1980. Notes on some fungi occurring on *Peltigera*, with a key to accepted species. *Trans. Br. mycol. Soc.* **74**: 363–386.

—— 1982. Changes to the British checklist arising from the abolition of later fungal starting points. *Lichenologist* **14**: 131–137.

—— 1985*a*. A redisposition of the species referred to the ascomycete genus *Microthelia*. *Bull. Br. Mus. nat. Hist.* (Bot.) **14**: 43–181.

—— 1985*b*. Problems and prospects in the systematics of the Ascomycotina. *Proc. Indian Acad. Sci.* (Plant sci.) **94**: 319–339.

—— 1987. The evolution and adaptation of sexual reproductive structures in the Ascomycotina. *In* A. D. M. Rayner, C. M. Brasier & D. Moore (Eds) *Evolutionary biology of the fungi* [BMS symposium **12**: 179–189]. Cambridge.

—— 1988*a*. The variety of fungal-algal symbioses, their evolutionary significance, and the nature of lichens. *Bot. J. Linn. Soc.* **96**: 3–20.

—— 1988*b*. Coevolution of fungi with algae and cyanobacteria in lichen symbiosis. *In* D. L. Hawksworth & C. Pirozynsky (Eds) *Coevolution of fungi with plants and animals*: 125–148. London.

—— **& Eriksson, O.** 1988. 895–906 Proposals to conserve 11 family names in the Ascomycotina (Fungi). *Taxon* **37**: 190–193.

—— **& Hill, D. J.** 1984. *The lichen-forming fungi*. Glasgow.

—— **James, P. W. & Coppins, B. J.** 1980. Checklist of British lichen-forming, lichenicolous and allied fungi. *Lichenologist* **12**: 1–115.

—— **& Sherwood, M. A.** 1982. Two new families in the Ascomycotina. *Mycotaxon* **16**: 262–264.

—— **Sutton, B. C. & Ainsworth, G. C.** 1983. *Ainsworth & Bisby's Dictionary of the Fungi*. 7th ed. Kew.

Henssen, A. & Jahns, H. M. 1974. *Lichenes: Eine Einführung in die Flechtenkunde*. Stuttgart.

Hitch, C. J. B. & Cayton, P. 1986. *Sarcopyrenia gibba* [New, rare or interesting British lichen records]. *Bull. Br. lichen Soc.* **59**: 32.

Holm, L. 1957. Etudes taxonomiques sur les Pléosporacées. *Symb. bot. upsal.* **14**(3): 1–188.

Holm, K. & Holm, L. 1977. Nordic junipericolous ascomycetes. *Symb. bot. upsal.* **21**(3): 1–70.

Holmgren, P. K., Keuken, W. & Schofiels, E. K. 1981. *Index herbariorum, part 1: Herbaria of the world*, 7th ed. Utrecht.

Honegger, R. 1984. Ultrastructural studies on conidiomata, conidiophores, and conidiogenous cells in six lichen-forming ascomycetes. *Can. J. Bot.* **62**: 2081–2093.

Janex-Favre, M. C. 1968. L'ontogénèse des ascocarpes et la position systématique du mycobionte du lichen *Arthopyrenia fallax* (Nyl.) Am. *Bull. Soc. bot. Fr.* **115**: 359–368.

—— 1970. Recherches sur l'ontogénie, l'organisation et les asques de quelques Pyrénolichens. *Rev. bryol. lichén.* II, **37**: 421–649.

—— 1981. Etudes ontogéniques chez le *Porina byssophila* (Pyrénolichen) II. Les périthèces. *Cryptogamie, Bryol. lichén.* **2**: 253–275.
Jensen, J. D. 1985. Peridial anatomy and pyrenomycete taxonomy. *Mycologia* **77**: 688–701.
Johnson, G. T. 1959. The Trypetheliaceae of Mississipi. *Mycologia* **51**: 741–750.
Johnston, A. & Booth, C. (Ed.) 1983. *Plant Pathologist's Pocketbook*, 2nd ed. Slough.
Keissler, K. 1930. Die Flechtenparasiten. *Rabenh. Krypt., Fl.* **8**: i–xi, 1–712. Leipzig.
—— 1938. Pyrenulaceae, Mycoporaceae, Coniocarpineae. *Rabenh. Krypt., Fl.* **9**, 1(2): i–x, 1–846. Leipzig.
Kondratyuk, S. Ya. 1985. Nobi ta ridkisni dlya likhenflori URSR vidi lninainikiv. *Ukranyinskyi Botanichnyi Zhurnal* **42**(4): 67–70.
Kopaczevskaja, E. G., Makarevicz, M. F. & Oxner, A. N. (Eds) 1977. *Opredeliditel' lishainikov SSSR* **4**: *Verrucariaceae—Pilocarpaceae*. Leningrad.
Körber, G. W. 1855. *Systema lichenum Germaniae (Die Flechten Deutschlands)*. Breslau.
—— 1859–1865. *Parerga lichenologica*. Breslau.
Korf, R. P. 1958. Japanese discomycete notes I–VIII. *Sci. Rep. Yokohama natn. Univ.* II, 7: 7–35.
Krempelhuber Monacensi, A. de 1873. Symbolae ad floram Brasilae centralis cognoscendam, edit. Engwarming. Particula XIV (Lichenes Brasiliensis enumerati et descripti). *Vidensk. Meddel. Naturh. Foren. Kjöbenhaum* **5**: 1–35.
Kusan, F. 1953. *Prodromus flore Lisaja Jugoslavije*. Zagreb.
Lamarck, J. B. A. P. M. de & De Candolle, A. P. 1805. *Flore française*, 3rd ed., **2**. Paris.
Lamb, I. M. 1963. *Index nominum lichenum inter annos 1932 et 1960 divulgatorum*. New York.
Lanjouw, J. et al. 1956. *International code of botanical nomenclature adopted by the Eighth International Botanical Congress, Paris, July 1954*. Utrecht.
Laundon, J. R. 1979. Deceased lichenologists: their abbreviations and herbaria. *Lichenologist* **11**: 1–26.
Lundqvist, N. 1973. Nordic Sordariaceae s. lat. *Symb. bot. upsal.* **20**(1): 1–374.
Luttrell, E. S. 1951. Taxonomy of the Pyrenomycetes. *Univ. Miss.. Stud.* **24**: 1–120.
—— 1965. Paraphysoids, pseudoparaphyses, and apical paraphyses. *Trans. Br. mycol. Soc.* **48**: 135–144.
—— 1973. Loculoascomycetes. *In* G. C. Ainsworth, F. K. Sparrow & A. S. Sussman (Eds) *The Fungi: an advanced treatise* **4**: 135–219. London.
Magnusson, A. H. 1936. *Förteckning över Skandinaviens Växter,* **4**. Lavar. Lund.
Malbranche, A. F. 1869. Catalogue descriptif des lichens de la Normandie. *Bull. Soc. Amis Sci. nat. Rouen* **5**: 248–322.
Massalongo, A. 1852. *Ricerche sull' autonomia dei licheni Crostosi*. Verona.
—— 1855. *Symmicta lichenum novorum vel minus cognitorum*. Verona.
—— 1856. *Miscellanea lichenologica*. Verona.
—— 1860. Esame comparativo di alcuni generi di licheni. *Atti Ist. veneto Sci.* III, **5**: 313–337.
Mayrhofer, H. & Poelt, J. 1985. Die Flechtengattung *Microglaena* sensu Zahlbruckner in Europa. *Herzogia* **7**: 13–79.
Minter, D. W. & Cannon, P. F. 1984. Ascospore discharge in some members of the Rhytismatiaceae. *Trans. Br. mycol. Soc.* **83**: 65–92.
—— **Sutton, B. C. & Brady, B. L.** 1983. What are phialides anyway? *Trans. Br. mycol. Soc.* **81**: 109–120.
Moruzi, C., Petria, E. & Mantu, E. 1967. Catalogul lichenitor din România. Lucr. Grad. bot. Buc. **1967**: 1–389.
Müller, E. 1981*a*. The bitunicate ascus. *In* D. R. Reynolds (Ed.) *Ascomycete systematics: the Luttrellian concept*: 49–53. New York.
—— 1981*b*. Relations between conidial anamorphs and their teleomorphs. *In* G. T. Cole & B. Kendrick (Eds) *Biology of conidial fungi* **1**: 145–169. London.
—— 1987. 461. *Zignoella* (Sacc.) Sacc. *In* Eriksson, O. & Hawksworth, D. L. Notes on Ascomycetes systematics, 225–463. *Systema Ascomycetum* **6**: 156.
—— **& von Arx, J. A.** 1962. Die Gattung der didymosporen pyrenomyceten. *Beitr. Kryptogamenflora Schweiz* **11**(2): 1–922.
—— **& Defago, G.** 1966. *Beloniella* (Sacc.) Boud. und *Dibeloniella* Nannf., zwei wenig bekannte Discomycetengattungen. *Sydowia* **20**: 157–168.
—— **Petrini, O., Fisher, P. J., Samuels, G. J. & Rossman, A. Y.** 1987. Taxonomy and anamorphs of the Herpotrichiellaceae with notes on generic synonymy. *Trans. Br. mycol. Soc.* **88**: 63–74.
Müller Argoviensis, J. 1862. Principes de classification des lichens et énumération des lichens de Génève. *Mem. Soc. Phys. Hist. nat. Génève* **16**: 343–433.
—— 1885. Pyrenocarpeae Cubenses a cl. C. Wright lectae. *Bot. Jb.* **6**: 374–421.
—— 1892. Lichenes exotici. *Hedwigia* **31**: 276–288.
Nannfeldt, J. A. 1932. Studien über die Morphologie und Systematik der nicht lichenisierten inoperculaten Discomyceten. *Nova Acta R. Soc. Scient. upsal.* IV, **8**(2): 1–368.
—— 1976. Iodine reactions in ascus plugs and their taxonomic significance. *Trans. Br. mycol. Soc.* **67**: 283–287.
Navarro-Rosinés, P. & Hladún, N. L. 1990. El género *Sarcopyrenia* Nyl. (hongos liquenícolas) en Europa y norte de Africa. *Candollea* **45**: 469–489.
Norman, J. M. 1853. Conatus praemissus redactionis novae generum nonnullorum lichenum in organis fructificationis vel sporis fundatae. *Nytt Magaz. Naturvid.* **7**: 213–252.
—— 1868. Lichenes Finnmarkici novi. *Bot. Notiser* **1868**: 191–193.
—— 1884. Nova genera et species lichenum Florae Norvegicae. ö *fvers. K. VetenskAkad. Förh.* **41**: 31–42.
De Notaris, G. 1846. Frammenti lichenografici di un lavoro inedito. *Nuovo G. bot. ital.* **2**: 174–224, 299–330.
Nylander, W. 1858. Expositio synoptica pyrenocarpeorum. *Mém. Soc. Acad. Maine-et-Loire* **4**: 5–88.
—— 1861. Lichenes scandinaviae. *Notis. Sällsk. Faun. Fl. fenn. Förh.* **2**: 1–312, tb 1
—— 1864. Pyrenocarpei guidam Europaei novi. *Flora, Jena* **47**: 353–358.
—— 1873. Bidrag till Sydöstra Tavastlands Flora: Lichenes. *Notis. Sällsk. Faun. Fl. fenn. Förh.* **11**: 314–348.
—— 1876. Circa Pyrenocarpeos in Cuba collectos a cl. C. Wright. *Flora, Jena* **59**: 364–365.
Oliver, E. M., Bridge, P. D. & Hawksworth, D. L. 1987. The effect of selected mountants and stains on the measurement of fungal spores. *Mycopath.* **97**: 165–172.
Parguey-Leduc, A. 1977. Les asques des Pyrénomycètes. *Revue Mycol.* **41**: 281–337.
—— **& Janex-Favre, M. C.** 1982. La paroi des asques chez les Pyrénomycètes: étude ultrastructurale, I. Les asques bituniqués typiques. *Can. J. Bot.* **60**: 1222–1230.
—— —— 1984. La paroi des asques chez les Pyrénomycètes: études ultrastructurale, II. Les asques unituniqués. *Cryptogamie, mycol.* **5**: 171–187.
Poelt, J. 1969. *Bestimmungsschlüssel Europäischer Flechten*. Lehre: J. Cramer.
—— 1974 ['1973']. Appendix A: Classification. *In* V. Ahmadjian & M. E. Hale (Eds) *The lichens*: 599–632. London.
Rabenhorst, L. 1850. Vorläufiger botanischer Bericht über meine Reise durch die östlichen und südlichen Provinzen Italiens. *Flora, Jena* **33**: 305–320, 322–325, 338–349, 355–363, 372–383, 390–399.
—— 1850. Systematische Uebersicht der auf meiner italienischen Reise beobachteten Kryptogamen. *Flora, Jena* **33**: 529–537.
Rehm, H. 1881. Ascomyceten. *Ber. nat. Ver. Augsburg* **26**: 1–132.
Richardson, D. H. S. 1971. Lichens. *In* C. Booth (Ed.) *Methods in microbiology* **4**: 267–293. London.
—— **& Morgan-Jones, G.** 1964. Studies on lichen asci, I. The bitunicate type. *Lichenologist* **2**: 205–224.
Riedl, H. 1962. Die Arten der Gattung Mycoporellum Müll. Arg. sensu A. Zahlbruckner, Catal., nebst Bemerkungen zum System dothidealer Flechten. *Sydowia* **15**: 257–287.
—— 1963. Die Arten der Gattung Mycoporellum Müll. Arg. sensu A. Zahlbruckner, Catal., nebst Bemerkungen zum System dothidealer Flechten. *Sydowia* **16**: 215–262.
Rollins, R. C. 1972. The need for care in choosing lectotypes. *Taxon* **21**: 635–637.
—— 1980. On the process of lectotypification. *Rhodora* **82**: 509–511.
Rossman, A. Y. 1983. The phragmosporous species of *Nectria* and related genera (*Calonectria, Ophionectria, Paranectria, Scoleconectria* and *Trichonectria*). *Mycol. Pap.* **150**: 1–164.
Sampaio, G. 1923. Novos materiais para a liquenologia Portuguesa. *Bolm Soc. brot.* II, **2**: 161–179.
Santesson, R. 1952. Foliicolous lichens I. A revision of the taxonomy of the obligately foliicolous lichenized fungi. *Symb. bot upsal.* **12**: 1–590.
—— 1953. The new systematics of lichenized fungi. *In* H. Osvald & E. Aberg (Eds) *Proceedings of the Seventh International Botanical Congress, Stockholm*: 809–810. Stockholm.
—— 1960. Lichenicolous fungi from northern Spain. *Svensk bot. Tidskr.* **54**: 499–522.
—— 1984. *The lichens of Sweden and Norway*. Stockholm.
Sherwood, M. A. 1977*a*. The Ostropalean fungi. *Mycotaxon* **5**: 1–277.
—— 1977*b*. A non–lichenized species of *Ramonia*. *Mycotaxon* **6**: 186–188.
—— 1981. Convergent coevolution in discomycetes from bark and wood. *Bot. J. Linn. Soc.* **82**: 15–34.
—— **Hawksworth, D. L. & Coppins, B. J.** 1980. *Skyttea*, a new genus of odontotremoid lichenicolous fungi. *Trans. Br. mycol. Soc.* **75**: 479–490.
Sherwood-Pike, M. A. 1987. The Ostropalean fungi III: The Odontotrematceae. *Mycotaxon* **28**: 137–177.
—— **& Boise, J.** 1986. Studies in lignicolous ascomycetes: *Xylopezia* and *Mycowinteria*. *Brittonia* **38**: 35–44.
Shoemaker, R. A. 1976. Canadian and some extralimital *Ophiobolus* species. *Can. J. Bot.* **54**: 2365–2404.
Smith, A. L. 1911. New lichens. *J. Bot., Lond.* **49**: 41–44.
Sommerfelt, S. C. 1826. *Supplementum Florae lapponicae*. Christianiae.
Stirton, J. 1878. Remarks on Mr. Crombie's paper on the *Challenger* lichens. *J. Linn. Soc.,* (Bot.) **17**: 152–157.
Sussman, A. S. & Halvorsson, H. O. 1966. *Spores: their dormancy and germination*. New York.
Swinscow, T. D. V. 1962. Pyrenocarpous lichens, 3. The genus *Porina* in the British Isles. *Lichenologist* **2**: 6–56.
—— 1965. Pyrenocarpous lichens, 9. Notes on various species. *Lichenologist* **3**: 72–83.

Theissen, F. 1916. Mykologische Abhandlungen. *Verh. zool.-bot. Ges. Wien* **66**: 296–400.
Thor, G. 1990. The lichen genus *Chiodecton* and five allied genera. *Opera Botanica* **103**: 1–92.
Trevisan, V. 1860. *Conspectus Verrucarinarum*. Bassano.
—— (1861) Synopsis generum Trypethelinarum. *Flora, Jena* **44**: 17–25.
Triebel, D. 1989. Lecideicole Ascomyceten. Eine Revision der obligat lichenicolen Ascomyceten auf lecideoiden Flechten. Bibl. lichenol. **35**: 1–278. Berlin.
Vainio, E. A. 1883. Adjumenta ad lichenographiam Lapponiae fennicae atque Fenniae borealis, II. *Meddn Soc. Fauna Flora fenn.* **10**: 1–230.
—— 1890. Etude sur la classification naturelle de la morphologie des lichenes du Brésil. *Acta Soc. Fauna Flora fenn.* **7**: 1–247; 1–256.
—— 1915. Additamenta ad lichenographiam Antillarum illustrandam. *Suomal. Tiedeakat. Toim.* A, **6**: 1–226.
—— 1921. Lichenographia Fennica I: Pyrenocarpaceae. *Acta Soc. Fauna Flora fenn.* **49**(2): 1–274.
Vobis, G. & Hawksworth, D. L. 1981. Conidial lichen-forming fungi. *In* G. T. Cole & B. Kendrick (Eds) *Biology of conidial fungi* **1**: 245–273. London.
Vouaux, L. 1913. Synopsis des champignons parasites des lichens. *Bull. Soc. mycol. Fr.* **29**: 33–128.
Walker, J. 1980. *Gaeumannomyces, Linocarpon, Ophiobolus* and several other genera of scolecospored ascomycetes and *Phialophora* conidial states, with a note on hyphopodia. *Mycotaxon* **11**: 1–129.
Wirth, V. 1980. *Flechtenflora*. Stuttgart.
Zahlbruckner, A. 1921–22, 1924, 1932. *Catalogue lichenum universalis* **1**, **2**, **8**. Leipzig.
—— 1926. Lichens (Flechten). B. Spezieller Teil. *In* [H. G.] A. Engler (Ed.) *Nat. Pflanzenfam.* **8**: 61–270. Leipzig.
—— 1935. Lichenes: Nomen genericum sec. regulas rejiciendum. *In* J. Briquet (Ed.) *International rules of botanical nomenclature adopted by the International Botanical Congresses of Vienna, 1905, and Brussels, 1910, revised by the International Botanical Congress, Cambridge, 1930*: 127–129. Jena.
Zalasky, H. 1968. *Rhytidiella moriformis* n.gen., n.sp. causing rough-bark of *Populus balsamifera*. *Can. J. Bot.* **46**: 1383–1387.

INDEX

Acanthostigmella 177
Acer 147, 148, 151
acerina (**Cresporhaphis**) 89, 147–149, 151, 155
acerina (*Leptorhaphis*) 147
aciculifera (*Leptorhaphis*) 87, 134, 135
aciculifera (*Melanotheca*) 134, 135
aciculifera (*Tomasellia*) 134
aciculiferum (*Athrismidium*) 134
aciculiferum (**Celothelium**) 87, 132, 134–5, 138
adspersa (*Microthelia*) 99, 101, 102
affinis (*Porina*) 175
affinis (Strigula) 175
aggregata (Melanotheca) 132
aggregata (*Verrucaria*) 132
aggregatus (*Leptorhapis*) 149, 151, 152
agminella (*Melanotheca*) 132
alba (Betula) 110, 169
alba (Populus) 122, 173
albissima (*Leptorhaphis*) 110
albissima (*Verrucaria*) 106, 107, 109, 178
albissima var. *minutissima* (*Verrucaria*) 178
Alnus 129
alnus (Frangula) 126
amygdali (*Campylacia*) 97
amygdali (*Leiophloea*) 97
amygdali (Leptorhaphis) 97–99
amygdali (*Sagedia*) 97, 99
amygdali (*Verrucaria*) 97, 98
amygdalus (*Prunus*) 97, 99
analepta (*Arthopyrenia*) 96, 124
analepta var. *atomaria* (*Arthopyrenia*) 99
analeptus (*Lichen*) 87, 96, 124
Anisomeridium 123
anomala (Melanotheca) 132
anomala (Pyrenula) 132
anomalum (*Trypethelium*) 132
aquatica (*Gongylia*) 171
aquatica (Sagediopsis) 171
aquifolium (Ilex) 105, 141, 158
argena (Phlyctis) 158
armorica (*Leptorhaphis*) 163
armorica (*Verrucaria*) 163, 164
Arthonia 184
Arthopyrenia 86, 87, 89, 90, 91, 92, 94, 95, 96, 97, 107, 114, 116, 123–131, 141, 168, 184
Arthopyrenia sect. *Leptorhaphis* 94
Arthopyrenia sect. *Campylacia* 94
Arthopyrenia sect. *Leptorhaphis* 87
Arthopyreniomyces 96
athalina (*Ramonia*) 181
Athrismidium 135
atomaria (*Arthopyrenia*) 99
atomaria (*Campylacia*) 99, 102, 103
atomaria (*Didymella*) 99
atomaria (*Didymosphaeria*) 99
atomaria (*Leptorhaphis*) 86, 87, 90, 92, 96, 97, 99–103, 108, 109, 114, 122, 123, 172, 178
atomaria (*Microthelia*) 94, 99
atomaria (*Mycomicrothelia*) 99
atomaria (*Verrucaria*) 99, 101
atomaria f. *laricis* (*Leptorhaphis*) 110
atomariae (*Microtheliomyces*) 94, 99
atomarium (*Tichothecium*) 99
atomarius (*Lichen*) 87, 99, 101, 123
avellana (Corylus) 114, 115, 116, 141, 143
avium (Prunus) 118

babylonica (Salix) 156
bacillispora (Sarcopyrenia) 159
Baeomyces 96
baranyany (Rhytidiella) 167
barbara (Sagediopsis) 87, 183, 184
barbara (*Segestria*) 184
barbarus (*Ophiobolus*) 87, 171, 184
beckhausiana (*Leptorhaphis*) 87, 159, 160
beckhausiana (Sarcopyrenia) 87, 159–161, 162, 164
beloniza (*Arthopyrenia*) 164
beloniza (*Leptorhaphis*) 164
beloniza (**Rhytidiella**) 89, 165, 166, 167
beloniza (*Verrucaria*) 164–167
Betula 86, 97, 103, 105, 106, 107, 109, 110, 141, 157, 158, 169, 170
betulus (Carpinus) 158
biforme (Anisomeridium) 123
borealis (Quercus) 103
borreri (Porina) 174, 175
buxi (**Celothelium**) 132, 135–137, 139, 141
buxi (*Leptorhaphis*) 135
byssacea var. *minutissima* (*Verrucaria*) 177–178
byssacea var. *sticticа* (*Verrucaria*) 156, 184
byssophila (Porina) 93

Calicium 171
Caloplaca 101
campestre (Acer) 147, 148
Campylacia 86, 87, 94, 96, 132, 172
candida (*Leptorhaphis*) 167–169
candida (**Stictis**) 168, 169
Capronia 93, 177
carneola (Pachyphiale) 158
Carpinus 157
carrollii (*Leptorhaphis*) 139, 141
cascarillae (*Verrucaria*) 96
Celothelium 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 131–146, 178
cembra (Pinus) 181
cembrina (Arthopyrenia) 129
cerasi (Arthopyrenia) 97, 126, 127
cerasi (*Endophis*) 86, 87, 94, 117, 118
cerasus (Prunus) 118
Chaetosphaeria 147
chlarotera (Lecanora) 154
cicatricosa (Glyphis) 138
Cinchona 137
cinchonarum (Celothelium) 87, 132, 133, 135, 137–139
cinchonarum (*Leptorhaphis*) 87, 137
cinchonarum (*Tomasellia*) 137
cinerescens (Arthopyrenia) 131
Chiodecton 132

Chloridium 147
Coenoicia 132
confertior (Leptorhaphis) 104, 105, 106
confusa (Mycomicrothelia) 141
contigua (*Lecidea*) 184
contorta (Aspicilia) 161
contorta (Leptorhaphis) 97, 103, 104, 105, 108, 111, 113, 116, 118, 121
Corylus 97, 116, 141, 142, 143
crassa (Enterographa) 175
Cresporhaphis 86, 87, 89, 90, 91, 92, 93, 95, 147–156, 169, 184
cylindrospora (*Leptorhaphis*) 161
cylindrospora (Sarcopyrenia) 159, 160, 161–162
cylindrospora (*Verrucaria*) 161

Daphne 97, 118, 120, 121
deformis (Leptorhaphis) 92, 96, 97, 103–105, 106
depressa (*Sagedia*) 96
detincta (*Didymosphaeria*) 139
dilatata (Populus) 121, 123
dominicana (*Leptorhaphis*) 87, 139
dominicanum (**Celothelium**) 87, 132, 139, 140, 141
dulcis (Prunus) 97, 98

elaeochroma (Lecidella) 154
elegans (Graphis) 135
Endophis 86, 94, 96
epidermidis (*Arthopyrenia*) 105, 107
epidermidis (*Campylacia*) 105, 109
epidermidis (Leptorhaphis) 86, 87, 88, 89, 90, 92, 96, 97, 103, 105–110, 116, 178
epidermidis (*Lichen*) 86, 87, 96, 105
epidermidis (*Spermatodium*) 105
epidermidis (*Verrucaria*) 86, 96, 105, 107, 109, 110
epidermidis var. *albissima* (*Arthopyrenia*) 106
epidermidis var. *albissima* (*Verrucaria*) 96, 106, 107, 109, 110
epidermidis var. *analepta* f. *atomaria* (*Verrucaria*) 99
epidermidis var. *atomaria* (*Arthopyrenia*) 99
epidermidis var. *atomaria* (*Verrucaria*) 99
epidermidis var. *fusispora* (*Verrucaria*) 107
epidermidis var. *lunulata* (*Verrucaria*) 122–123
epidermidis var. *olivetorum* (*Leptorhaphis*) 116, 177, 178
epidermidis var. *tremulae* (*Verrucaria*) 121
epidermidis var. *vulgaris* (*Verrucaria*) 105, 110
epidermidis f. *fusispora* (*Verrucaria*) 107
erythrospora (Nodulosphaeria) 169
erythrosporus (*Ophiobolus*) 169
euphorea (Lecidea) 123
europea (Olea) 116
excelsior (Fraxinus) 101, 131

faginea (*Porina*) 175
fallax (*Arthopyrenia*) 89
fragilis (Salix) 154, 155, 156
franconium (*Physma*) 174
frangula (*Rhamnus*) 126, 127
Fraxinus 99, 101, 129, 131, 142
fusca (Stictis) 169

geisleri (*Lithosphaeria*) 87, 158, 159, 163, 164
gelatinosa (Tomasellia) 135
gelatinosum (*Athrismidium*) 135
germanica (Genista) 110, 111
gibba (*Leptorhaphis*) 163
gibba (Sarcopyrenia) 87, 158, 159, 161, 162, 163–164
gibba (*Verrucaria*) 158, 163
gibba var. geisleri (Sarcopyrenia) 159, 164
gibba var. gibba (Sarcopyrenia) 164
glaucophaea (Porpidia) 181, 183, 184
glomerulosa (*Lecidea*) 123
glutinosa (Alnus) 124, 126, 129, 176, 177

hemisphaerica (Xylopezia) 93
himalayensis (*Tomasellia*) 132
hypoleucum (Chiodecton) 138

Ilex 97, 104, 158
inflatus (Ophiobolus) 169, 170, 171
ischnobela (*Leptorhaphis*) 139
ischnobela (*Melanotheca*) 139, 141
ischnobela (*Tomasellia*) 139
ischnobelum (**Celothelium**) 92, 134, 135, 137, 139–143, 158

Karschia 86
kentrospora (*Leptorhaphis*) 169
kentrospora (*Verrucaria*) 169–171, 172
koerberi (*Leptorhaphis*) 169, 171
koerberi (*Leptosphaeria*) 171
koerberi (*Metasphaeria*) 171
koerberi (*Ophiobolus*) 171
koerberi (*Sagediopsis*) 171
kunzei (*Calicium*) 171
kunzei (Lahmia) 171–173, 178
kunzei var. *ecrustacea* (*Lahmia*) 178
kunzei (*Pragmopora*) 171

laburni (Arthopyrenia) 129
Lahmia 89, 94, 178
Lahmiomyces 94
lapponina (Arthopyrenia) 89, 184
laricis (**Leptorhaphis**) 97, 103, 105, 110–111, 112
Larix 97, 110, 111
Lasiosphaeriopsis 93, 159
Lecanora 101, 149
lepadinum (Thelotrema) 158
leprieurii (Celothelium) 132
leptalea (Porina) 154
leptogiophila (*Leptorhaphis*) 174–175
leptogiophila (*Leptosphaeria*) 174
leptogiophila (*Metasphaeria*) 174
leptogiophila (Physalospora) 174
Leptomycorhaphis 94
Leptorhaphiomyces 94
Leptorhaphis 86, 87, 88, 89, 90, 91, 92, 93, 94–123, 124, 132, 139, 147, 167, 175, 177, 178, 184, 185
Leptorhaphis sect. *Dimidiatae* 87
Leptorhaphis sect. *Integrae* 87, 93, 146
Leptorhaphis subgen. *Campylacia* 87, 94
Leptohaphis subgen. *Tomasellia* 87
Leptosphaeria 87, 167
leptosporum (Chiodecton) 132
Lithosphaeria 87, 158, 159
longispora (*Leptorhaphis*) 175
longispora (*Verrucaria*) 174, 175
longonigra (**Capronia**) 175, 177
longonigra (*Leptorhaphis*) 176–177
lucida (*Arthopyrenia*) 111
lucida (Leptorhaphis) 87, 92, 96, 97, 101, 103, 105, 111–114, 123, 172, 178
lutea (Betula) 110
lycioides (Rhamnus) 116
lyrata (Arthopyrenia) 126

macrocyrtospora (*Arthopyrenia*) 164
macrocyrtospora (*Leptorhaphis*) 164
macrocyrtospora (*Verrucaria*) 164, 166
macrospora (**Cresporhaphis**) 147, 149–151, 169, 179
macrosporum (Thelotrema) 143
maggiana (*Campylacia*) 114, 179
maggiana (Leptorhaphis) 97, 112, 114–116, 179
maggiana (*Verrucaria*) 114
maggianae (*Leptorhaphiomyces*) 94, 114
maggianum (*Spermatodium*) 114
mahleb (Prunus) 117
melanospora (Mycomicrothelia) 101
Melanotheca 87, 131, 132
Melanotheca sect. *Celothelium* 131
Metasphaeria 175
mezereum (Daphne) 120, 121
Micarea 86, 151
michaudi (*Leptorhaphis*) 116, 177, 178
Microglaena 86
Microtheliomyces 94
microspila (Arthopyrenia) 178
microspilum (Stigmidium) 178
Microthelia 86, 101
Microthelia [sect.] *Atomariae* 94
miculiformis (Mycomicrothelia) 139
minutissima (*Verrucaria*) 178
moriformis (Rhytidiella) 165, 167
mosigii (*Calicium*) 171

muelleri (Cresporhaphis) 89, 90, 105, 147, 148, 149, 151–152, 155, 156
muelleri (*Leptosphaeria*) 151
muelleri (*Sphaeria*) 151
Mycoglaena 94, 171
Mycoleptorhaphis 94
Mycomicrothelia 89, 92, 96, 101
Mycoporellum 132
Mycoporopsis 132
Mycowinteria 149
myricae (Mycoglaena) 88, 171, 172
myriospora (*Verrucaria*) 139, 141

nigra (Populus) 102, 114, 122, 123
nigra (Sambucus) 101
Nodulosphaeria 169
novae-guineae (*Leptorhaphis*) 178
nuda (*Coenoicia*) 132
nudum (*Celothelium*) 132
nudum (*Trypethelium*) 132

Odontotrema 181
Odontura 89, 90, 91, 92, 93
Olea 97, 116
oleae (Leptorhaphis) 97, 116–117, 118, 177, 178
oleae (*Limboria*) 116
oleae (*Sagedia*) 94, 96, 116
oleander (Nerium) 116, 117
olivacea (*Porina*) 96, 175
olivacea (*Verrucaria*) 96
olivaceae (Melanietum) 110
olivatra (Arthopyrenia) 124–126
olivatra (*Leptorhaphis*) 124
Ophiobolus 87, 110, 167, 169, 184
ornus (Fraxinus) 167, 168
ovoidea (Zignoella) 147
oxyspora (*Arthopyrenia*) 106, 109
oxyspora (*Campylacia*) 105, 110
oxyspora (*Leptorhaphis*) 86, 94, 96, 105, 109, 116, 177
oxyspora (*Pyrenula*) 105, 110
oxyspora (*Sagedia*) 87, 94, 96, 106
oxyspora (*Segestrella*) 106
oxyspora (*Verucaria*) 94, 105, 107, 108, 109
oxyspora var. *albissima* (*Verrucaria*) 106
oxyspora var. *fusispora* (*Campylacia*) 107
oxyspora var. *minutissima* (*Verrucaria*) 177
oxyspora var. *psilotera* (*Leptorhaphis*) 118
oxyspora var. *tremulae* (*Arthopyrenia*) 121
oxyspora var. *tremulae* (*Verrucaria*) 121
oxysporae (*Leptomycorhaphis*) 94, 106
oxysporum (*Spermatodium*) 105

padi (Arthopyrenia) 129
pallida (Lecanora) 101
parameca (Leptorhaphis) 87, 89, 97, 98, 103, 111, 117–118, 119, 121
parameca (*Sagedia*) 117, 118
parameca (*Verrucaria*) 117
parameca f. *amygdali* (*Leptorhaphis*) 97
paramecum (*Spermatodium*) 117
parietina (Xanthoria) 101
Parmelia 149
patzaltii (*Leptorhaphis*) 178
pendula (Betula) 109
pensylvanica (Prunus) 118
perplexum (Chiodecton) 138
personii f. *atomaria* (*Arthopyrenia*) 99
Pertusaria 96
peuce (Pinus) 181
Phaeoseptoria 176
Physalospora 175
Picea 126, 127
picea (Pinus) 178
piceae (*Lahmia*) 177, 178, 179
piceae (Lahmiomyces) 177, 178, 179
pinicola (Cresporhaphis) 147, 149, 152–154
pinicola (*Leptorhaphis*) 152
Pinus 126, 127, 147, 152, 154
pithyophila (Arthopyrenia) 124, 126–127
pithyophila (*Pseudosagedia*) 126
pithyophila (*Leptorhaphis*) 126
populi (*Parkerella*) 171
populicola (*Verrucaria*) 99, 101
Populus 86, 92, 97, 101, 102, 103, 112, 113, 114, 121, 122, 123, 156, 167, 173, 178
Porina 93, 175
prasina (Micarea) 143
Prunus 97, 98, 103, 118
pseudoacacia (Robinia) 154
pseudoplatanus (Acer) 128, 129, 151
Pseudoseptoria 178
psilotera (*Campylacia*) 118
psilotera (Leptorhaphis) 97, 116, 118–121
psilotera (*Verrucaria*) 118
psilotera var. *vermifera* (*Campylacia*) 112, 114
pubescens (Betula) 109, 110
punctiformis (Arthopyrenia) 107, 116, 129, 141
punctiformis (*Didymella*) 107
punctiformis (*Verrucaria*) 129
punctiformis var. *acerina* (*Pyrenula*) 128, 129
punctiformis var. *atomaria* (*Arthopyrenia*) 99
punctiformis var. *atomaria* (*Leiophloea*) 99
punctiformis var. *atomaria* (*Pyrenula*) 99
punctiformis var. *atomaria* (*Verrucaria*) 99
punctiformis var. *straminea* (*Verrucaria*) 184–185
pyramidalis (Populus) 123
Pyrenyllium 87, 96
pyrenopezizoides (*Leptorhaphis*) 180, 181
Pyrenula 87, 132
pyrenuloides (Arthopyrenia) 124

Quercus 97, 103, 116, 147, 150
quercus (*Campylacia*) 116, 178–181
quercus (*Leptorhaphis*) 116, 149, 150, 158, 178, 179
quercus (*Spermatodium*) 178
quercus (*Verrucaria*) 158, 178
quercus f. *koerberi* (*Leptosphaeria*) 171
quercus f. *macrospora* (*Leptorhaphis*) 149, 169, 179

Ramonia 181
repens (Glyphis) 138
Rhagadostoma 93, 159
Rhaphidicyrtis 86, 88, 89, 90, 91, 92, 93, 94, 95, 156–158, 179
rhaphidiza (*Melanotheca*) 135
rhaphidospora (*Beloniella*) 181
rhaphidospora (*Odontotremella*) 181
rhaphidospora (Odontura) 180, 181, 182
rhaphidospora (*Pyrenopeziza*) 181
rhaphidosporum (*Belonium*) 181
rhaphidosporum (*Odontotrema*) 181
rhyponta (Arthopyrenia) 123, 126
rhyponta (*Verrucaria*) 123
Rhytidiella 89, 94, 167
richeae (Meloderma) 90
robergia (*Metasphaeria*) 147, 148
Robinia 147
rubra (*Quercus*) 103
robur (Quercus) 115, 129, 149, 150, 154, 158, 175
rupestris (Verrucaria) 159

Sagedia 87, 94, 96
Sagedia subgen. *Campylacia* 86, 94, 96
Sagediopsis 90, 94, 171, 184
salicis (Arthopyrenia) 129
salicis (*Sagedia*) 86, 99, 101
Salix 97, 99, 101, 103, 105, 120, 121, 147, 154, 156, 178, 184
sambuci (Lecanora) 101
Sarcopyrenia 86, 87, 89, 90, 91, 93, 95, 158–164
Sarcopyreniomyces 159
Sarcopyreniopsis 159
Segestrella sect. *Endophis* 94
sempervirens (Buxus) 135, 137
serpentina (Graphis) 178
Skyttea 181
simplicella (*Melanotheca*) 132
socialis (Celothelium) 131, 132
socialis (*Verrucaria*) 131, 132
Spermatodium 96
sphenospora (*Campylacia*) 87, 121
sphenospora (*Leptorhaphis*) 121

sphenospora (*Verrucaria*) 121, 123
steinii (*Leptosphaeria*) 181
steinii (*Leptorhaphis*) 87, 171, 181–184
steinii (*Metasphaeria*) 181
steinii (*Ophiobolus*) 181
stenobela (*Verrucaria*) 143
stenobelum (Celothelium) 91, 132, 143–146
stenobola (*Leptorhaphis*) 143
stenomicra (*Arthopyrenia*) 184
stenomicra (*Leptorhaphis*) 184, 185
stenospora (Arthopyrenia) 124, 128–129
stenospora (*Leptorhaphis*) 128
stictica (*Limboria*) 184
stictica (*Pyrenothea*) 184
stictica (*Verrucaria*) 184
sticticum (*Cyphelium*) 184
sticticum var. *minutissium* (*Thrombium*) 114, 117
sticticus (*Lichen*) 184, 186
Stictis 89, 90, 93
Stictis sect. Cyclostoma 89, 169
stigmatella (Strigula) 175
stigmatella var. *atomaria* (*Verrucaria*) 99
stigmatella var. *tremulae* (*Verrucaria*) 122–123
straminea (*Arthopyrenia*) 184
straminea (*Leptorhaphis*) 184
straminea (*Verrucaria*) 184
Strigula 175, 178
subfurvum (Collema) 175
subfusca (Lecanora) 102
sylvestris (Pinus) 178

tartarea (Ochrolechia) 184
tartarina (Sagediopsis) 184
tartarina (*Verrucaria*) 184
Tilia 131
Tomasellia 87, 132
Tomasellia sect. *Celothelium* 131, 132
tremula (Populus) 99, 101, 102, 103, 112, 114, 123, 171, 173, 178
tremulae (*Arthopyrenia*) 121
tremulae (*Campylacia*) 86, 101, 103, 121
tremulae (Leptorhaphis) 86, 87, 91, 92, 96, 97, 101, 110, 114, 121–123, 178, 184
tremulae (*Mycoleptorhaphis*) 94, 121
tremulae (*Pyrenula*) 121, 123
tremulae (*Sagedia*) 103, 121
tremulae (*Spermatodium*) 103, 121
tremulae (*Verrucaria*) 121, 123
tremulae f. *laricis* (*Leptorhaphis*) 110
tremulae var. *lucida* (*Leptorhaphis*) 112
tremulae var. *sphenospora* (*Leptorhaphis*) 121
tremulicola (*Leptorhaphis*) 99
Trentepohlia 107, 141, 146, 154, 175
trichosporella (*Leptorhaphis*) 157
trichosporella (Rhaphidicyrtis) 156–158, 179
trichosporellum (*Mycoporellum*) 157
trichosporellum (*Mycoporum*) 156–157, 158
tumidula (Arthonia) 143

Ulmus 156
unicaudata (Rebentischia) 154
umbripicta (Arthopyrenia) 126, 129–131
umbripicta (*Leptorhaphis*) 129

Verrucaria 87, 93, 96
Verrucaria subgen. *Leptorhaphis* 94
vezdae (Bacidia) 141, 142

wienkampii (Cresporhaphis) 87, 89, 146, 147, 149, 151, 154–156, 184
wienkampii (*Leptorhaphis*) 87, 146, 154, 156
wienkampii var. *aggregata* (*Leptorhaphis*) 105, 151
wimmeriana (Koerberiella) 171
wolbecensis (*Leptorhaphis*) 157, 158

Xanthoria 91, 149
xylographoides (*Leptorhaphis*) 86, 117, 118
Xylopezia 93, 147

Zignoella 93, 147
Zignoina 93, 147
zollingeri (*Tomasellia*) 132

Bull. Br. Mus. nat. Hist. (Bot) **21**(2): 193–194 Issued 28 November 1991

The typification and identity of *Calymperes crassilimbatum* Renauld & Cardot (Musci: Calymperaceae).

L. T. Ellis

Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD

Reese (1991) placed *Calymperes loucoubense* Bescher. in synonymy with '*Calymperes crassilimbatum* Bescher.'. However, *C. crassilimbatum* was originally published by Renauld and Cardot (1894) and the parts of the type specimen in their herbaria (PC) represent a form of *Calymperes hispidum* Renauld & Cardot. This form has strongly-developed teniolae (sensu Ellis, 1990) which are continuous from the base to near the apex of the leaf. The papillae that cover the chlorophyllose lamina are easily discernible but do not attain the bristle-like proportions found in some collections of this species from Madagascar.

Calymperes hispidum Renauld & Cardot, *Bull. Soc. r. Bot. Belg.* **32** (2): 14 (1894).
Calymperes crassilimbatum Renauld & Cardot, *Bull. Soc. r. Bot. Belg.* **32** (2): 18 (1894), *syn. nov.*. Type: Réunion [Insula Bourbon], 1888, *Rev. Rodriguez* s.n. (PC!—lectotype, designated here; PC!—isolectotype).

An apparent isotype of *C. crassilimbatum* in Bescherelle's herbarium (BM) is *Syrrhopodon mahensis* Bescher. A detailed description of *C. hispidum* is given by Ellis (1988) and of *C.loucoubense* by Ellis (1991).

Key features of *Calymperes hispidum* and *C. loucoubense*

Cells of chlorophyllose lamina often up to 10 μm wide; in cross-section appearing peltate or like sharp canine teeth (Fig. 1c). Apices of gemmiferous leaves consisting of a narrow proboscis in which the costa is percurrent (Fig. 1a), gemmae produced from the ventral surface of the costal tip ..... **C. hispidum**
Cells of chlorophyllose lamina seldom more than 7.5 μm wide (rarely up to 10 μm); in cross-section seen to protrude bluntly from the ventral leaf surface, each protrusion tipped by a blunt, often flat-topped papilla; dorsal surface of cells flat and each with a similar papilla. Apices of gemmiferous leaves consisting of a shortly excurrent costa, gemmae produced from all around the costal tip .... **C. loucoubense**

Calymperes loucoubense Bescher. remains the correct name for a distinct species.

ACKNOWLEDGEMENTS. I am grateful to Dr Alan Harrington for his valuable comments on the manuscript and also thank Dr Helene Bischler-Causse for arranging the loan of specimens from Paris (PC).

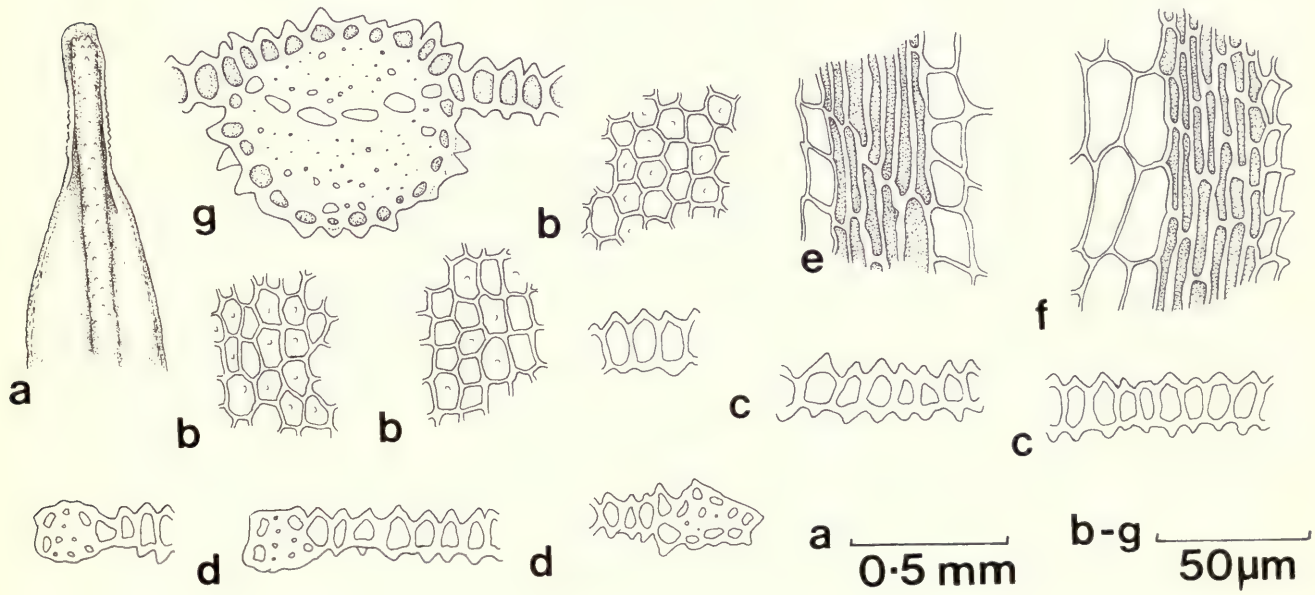


Fig. 1 *Calymperes crassilimbatum* Renauld & Cardot (= *C. hispidum*). a: apex of gemmiferous leaf in dorsal view; b, c: cells of chlorophyllose lamina (b: in surface view, c: in cross-section); d: margin of chlorophyllose lamina in cross-section; e, f: margin of hyaline leaf base (e: in mid-base, f: in distal base); g: costa at mid-leaf in cross-section. a–g Drawn from Bourbon, *Rodriguez* s.n. (PC).

REFERENCES

Ellis, L. T. (1988). Taxonomic notes on *Calympere*s II. *J. Bryol.* **15**, 127–140.
—— (1990). A taxonomic revision of *Calympere*s in southern India and neighbouring islands. *J. Bryol.* **15**: 697–732.
—— (1991). *Calympere*s *loucoubense* Besch., a distinct species from Madagascar. *J. Bryol.* **16**: 393–396.
Reese, W. D. (1991). *Syrrhopodon armatissimus* sp. nov. from Madagascar, with comments on other Calymperaceae from the Madagascar region. *Bryologist* **94**, 217–220.
Renauld, F. & Cardot, J. (1894 ['1893']). *Musci exotici novi vel minus cogniti*. IV. *Bull. Soc. r. Bot. Belg.* **32**(2), 8–40.

British Museum (Natural History) Publications

FLORA MESOAMERICANA

Flora Mesoamericana, a joint project of the Instituto de Biología, Universidad Nacional Autónoma de México, Missouri Botanical Garden, St. Louis, and The Natural History Museum London, will start in 1991 with the publication of Vol 6, covering half of the monocotyledonous families. The entire work will be in 7 volumes published in Spanish at approximately 2-yearly intervals. It will comprise a concise identification manual for the vascular plants of Mesoamerica. The work incorporates much new research and will form a data base for the floristics and taxonomy of the region.

A Preliminary Bibliography of the Mesoamerican Flora
R. J. Hampshire, D. A. Sutton

1988 245 × 175mm, 194pp,
0 565 01068 9 Paperback **£15.00**

THE CORALLINE RED ALGAE
An analysis of the genera and subfamilies of the nongeniculate Corallinaceae

W. J. Woelkerling

Nongeniculate coralline red algae (Corallinales, Rhodophyta) are both abundant in and vital to coral reefs, cementing the coral animal skeletons into a durable reef framework. In colder waters they form pavements of many square kilometres on the sea bed. It is one of the aims of this study to help resolve outstanding difficulties relating to taxonomy of the group. Extremely well illustrated with over 60 pages of scanning electron micrographs.

1988, 245 × 176mm, 268pp, 82 scanning electron micrographs, 259 figs, 19 tables.
Co-published with Oxford U.P.
0 198 54249 6 Hardback **£40.00**

Taxonomy and Biogeography of Macquarie Islands Seaweeds
R. W. Ricker.
1987, 175 × 250mm, 344pp, 126 figs.
0 565 00998 2 Hardback **£40.00**

SEAWEEDS OF THE BRITISH ISLES

Vol. 1. Part 1. Rhodophyta. Introduction, Nemaliales, Gigartinales. *P. S. Dixon & L. M. Irvine.*
1977, xi + 252pp, 90 figs.
0 565 00781 5 Paperback **£15.00**

Vol. 1. Part 2A. Cryptonemiales (*sensu stricto*), Palmariales, Rhodymeniales. *L. M. Irvine.*
1983, xii + 115pp, 28 figs.
0 565 00871 4 Paperback **£15.00**

Vol. 3. Part 1. Fucophyceae (Phaeophyceae). *R. L. Fletcher.*
1987, 145 × 210mm, 359pp, 90 figs, 15 plates.
0 565 00992 3 Paperback **£30.00**

Vol. 4. Tribophyceae (Xanthophyceae). *T. Christensen.*
1987, 145 × 210mm, 36pp, 8 figs.
0 565 00980 X Paperback **£7.50**

CONTENTS

81 **Early collections of the Holy Thorn (*Crataegus monogyna* cv. Biflora).**
A. R. Vickery

85 **A taxonomic study of the species referred to the ascomycete genus *Leptorhaphis*.**
Begoña Aguirre-Hudson

193 **The typification and identity of *Calymperes crassilimbatum* Renauld & Cardot (Musci: Calymperaceae).**
L. T. Ellis

Bulletin British Museum (Natural History)
BOTANY SERIES
Vol. 21 (2), November 1991